PELAGIC NITROGEN CYCLE IN AN ARCTIC LAKE

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PELAGIC NITROGEN CYCLE IN AN ARCTIC LAKE

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ABSTRACT

A mass balance for nitrogen was developed for the water column of Toolik Lake and the isotope tracers ^{15}N and ^{14}C were used to examine the phytoplankton ecology with respect to dissolved inorganic nitrogen (ammonium and nitrate).

The nutrient budget showed an oligotrophic ecosystem with important flux terms few and small in magnitude. Nitrogen input was primarily from inflowing rivers and was dominated by the dissolved organic fraction. Ammonium release from sediment provided the only other major source of nitrogen to the lake water. Toolik acted as a nitrogen sink, trapping 18% of the annual input. Retention was almost exclusively (98%) as dissolved organic nitrogen.

Tracer experiments suggested chronic nitrogen deficiency in the phytoplankton, but indigenous populations were well-adapted for utilizing characteristically low levels of nutrient. Phytoplankton showed a high affinity for both nitrate and ammonium as well as a lack of discrimination between the two forms of inorganic nutrient. The ambient concentration was the most important factor regulating uptake, with light and temperature of secondary importance.

More than 66% of the dissolved inorganic nitrogen supporting phytoplankton productivity was derived from local recycling, with the remainder from sediment efflux and riverine input. Dissolved organic nitrogen from inflowing waters probably provided an additional, important source of nutrient for the phytoplankton.

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CHAPTER 1. INTRODUCTION

Historic Perspective

Nitrogen has long been recognized as a macronutrient essential to phytoplankton nutrition (cf. early summaries by Hutchinson 1957; Syrett 1962). Initial studies concerning the relationship between dissolved inorganic nitrogen (DIN=NO_3^-+NH_4^+) and phytoplankton productivity consisted chiefly of spatial and temporal observations of nutrient and plant distributions (Pearsall 1932; Riley 1947). These data and corroborative laboratory investigations involving batch cultures of algal isolates (Ketchum 1939; Gerloff and Skoog 1954) gave initial, qualitative insight into DIN-phytoplankton interactions. However, the utility of these studies was severely handicapped by inadequate techniques for DIN analysis at typical ambient concentrations (Steele 1959) and the lack of associated supply and consumptive flux values (McCarthy 1980). Moreover, attempts at quantitatively assessing nitrogenous nutrient transformations by wet chemical techniques (i.e. temporal changes in extracellular nutrient levels) were unsuccessful. Failure was due to low rates of activity in unconcentrated natural samples of microorganisms relative to the precision of chemical methodology (McCarthy 1980; Harrison 1983).

The stable tracer ^{15}N was introduced nearly simultaneously to the study of nitrogenous nutrient utilization in lacustrine (Dugdale and Dugdale 1962) and marine (Dugdale et al. 1961) phytoplankton. Present knowledge concerning use and regeneration

of DIN derives almost exclusively from flux measurements involving this isotope over the last twenty years. These have focused on neritic and pelagic marine systems with comparatively little emphasis on fresh waters, perhaps because the rate of N supply is classically considered to regulate algal productivity in the former (Ryther and Dunstan 1971) and P is generally held to be most important in the latter (Schindler 1977).

The seminal paper by Dugdale and Goering (1967) forms the cornerstone for conceptual models of the pelagic nitrogen cycle in N-poor oceanic waters. Briefly, primary production was partitioned into "new" and "regenerated" components. New production was defined as that resulting from advective (river discharge, N-fixation, upwelling) injections of N to the euphotic zone while regenerated production was that from recycling of N within the surface water. Assuming that euphotic nitrification and N-fixation were negligible, new and regenerated primary production in the open ocean could be conveniently separated into fractions arising, respectively, from utilization of NO_3^- and NH_4^+.

Research to the late 1970's was directed toward understanding environmental regulators of N cycling dynamics in trophogenic waters of the ocean. Generally, these studies supported and refined the broad model proposed by Dugdale and Goering. For example, MacIsaac and Dugdale (1969) demonstrated that concentration-dependent uptake of DIN in natural phytoplankton assemblages could be described by Michaelis-Menten kinetics. In concert with

measured ambient DIN levels, this concept was successfully applied as a predictive tool (Epplev et al. 1969) to explain observed phytoplankton successional patterns off the Southern California coast. It was further extended by MacIsaac and Dugdale (1972) to include light-dependent utilization of DIN. An isotope dilution technique was introduced (Alexander 1970) to study community ammonification; subsequent investigations simultaneously assessing rates of ammonification and phytoplankton uptake of NH_4^+ showed that in the short-term (i.e. a few to several hours), marine primary production is supported by regenerated N. The analysis of enzymatic activity as an indicator of N source (Eppley and Coatsworth 1968) added a new dimension to studies of algal ecology. The importance of dissolved organic forms of nitrogen (DON) such as urea (McCarthy 1972) and amino acids (Schell 1974) in meeting phytoplankton nutrient requirements was established. A relative preference index was devised (McCarthy et al. 1977) as a measure of use versus availability for nitrogenous nutrients. Interactions of DIN (Conway 1977) and the influence of other nutrients (Harrison and Davis 1977) on NO_3^- and NH_4^+ utilization were explored. Finally, in an extension of the Dugdale and Goering model, Eppley and Peterson (1979) reviewed global productivity and ^{15}N uptake data and found that new primary production ranged from 6-46% of the annual total in various oceanic provinces.

Since the late 1970's, research has emphasized nitrogen cycling dynamics in nutrient-depleted euphotic waters on the

microscales of time and space (i.e. seconds and nanoliters). McCarthy and Goldman (1979) showed that short-term uptake of NH_4^+ in monospecific cultures of N-deficient marine algae far exceeded the growth rate. In a related study, Goldman et al. (1979) noted that in oligotrophic oceans where nutrients were at or below the limit of analytical detection, phytoplankton biomass was small but occurred in the Redfield ratio (atoms) of 106C:16N:1P. Furthermore, their laboratory studies showed that the Redfield ratio was attained only in plankton growing at a near-maximal rate. This led to the conclusion that phytoplankton in oligotrophic seas synthesize material at a maximum rate due to enhanced uptake capability when briefly exposed to transient, microscale nutrient pules generated, for example, by a feeding zooplankter. Enhanced short-term uptake capacity for NH_4^+ was subsequently demonstrated for natural algal populations (Glibert and Goldman 1981), reinforcing the concept of the microenvironment as the important dimension in phytoplankton-nutrient relationships.

On the other hand, opposing studies (Jackson 1980) refuted from a physical standpoint the ability of a nutrient pulse in a turbulent environment to exist long enough to serve as a viable nutrient source for phytoplankton.

Present investigations continue to stress the microenvironment by focusing on the relationship among phytoplankton, bacteria and microflagellates in oceanic nutrient cycling. Goldman (1984) has advanced the "spinning wheel" hypothesis, where amorphous ag-

gregates of organic matter formed by physicochemical and biologically-mediated processes serve as self-contained microhabitats. The resident assemblage of autotrophs and heterotrophs adhering or in close proximity to the aggregate presumably coexist by recycling nutrients in these oases of the nutrient-impoverished mixed layer. Quantification of this relationship (Goldman 1985) is underway and will likely be in the mainstream of research efforts for the immediate future with respect to nitrogen-phytoplankton interactions.

Study Objectives

The overall aim of this investigation was to assess the seasonality of supply and demand for nitrogen by phytoplankton in Toolik Lake, located in the Alaskan arctic, and to analyze physicochemical and intrinsic biological factors controlling distribution and phytoplankton use of N. Specific components included:

(1) Establishment of a nitrogen budget to identify important sources and losses for the phytoplankton.

(2) Determination of the individual influences of temperature and light on DIN utilization by the phytoplankton.

(3) Evaluation of the influence of other chemical factors (e.g. trace elements, vitamins, PO_4^{3-} etc.) on dissolved inorganic carbon ($DIC=CO_2+HCO_3^-+CO_3^{2-}$) and DIN uptake by the phytoplankton.

(4) Testing for a diel periodicity in algal utilization of DIC and DIN.

(5) Measurement of seasonal and depth variations of algal productivity in terms of DIC and DIN utilization, analysis of the nutritional status with respect to N and assessment of ecological adaptations of the phytoplankton for survival in an N-poor environment.

(6) Evaluation of pelagic ecosystem function in Toolik in the context of the conceptual models developed by Dugdale and Goering (1967) and Eppley and Peterson (1979) for N-depleted marine waters.

Research Justification

In fresh waters, comprehensive seasonal data for pelagic N cycling dynamics are sorely lacking. This information is given only for Castle Lake, California (Axler et al. 1982 and related papers) and Lake Kizaki, Japan (Takahashi and Saijo 1981 and related papers). Nonetheless, N cannot be dismissed as unimportant in regulating primary biosynthesis of lacustrine systems. In reviewing comprehensive elemental budgets, Smith (1984) challenged the tenet that N and P supply constrain marine and freshwater autotrophic production, respectively, by concluding that there was no inherent difference in nutrient deficiency between the two; in *any* system, dominance of material exchange by physical processes (advection and eddy diffusion) will lead to N deficiency while con-

trol by biochemical processes will result in P deficiency.

Although a remote, deep lake in the arctic may seem a poor candidate for a detailed investigation of the pelagic N cycle for fresh waters, this choice can be defended from several standpoints.

Reviews of arctic limnology (Hobbie 1973, 1984) underscore the scarcity of even baseline information for this biogeographic province. However, increased public access by road to the Alaskan arctic and the attendant threat of anthropogenic alterations of natural nutrient cycles attest to the urgency for detailed physicochemical and biological studies. The meager data available point to the fragility of deep arctic lakes. Canadian Char Lake showed the lowest primary productivity of any major freshwater studied worldwide while culturally eutrophied Meretta Lake, located nearby, had chlorophyll (biomass) and annual productivity values 20 and 3 times higher (Kalff and Welch 1974).

The simplicity of an arctic lacustrine ecosystem argues for its selection as a convenient starting point for elucidating major controls and fluxes in the pelagic N cycle of lakes and offers advantages that far outweigh the disadvantages imposed by distance from the home base. These include a hypolimnion that may remain oxic year-round, the absence of heterocystous cyanobacteria from the plankton, a pristine environment with nutrient cycles uninfluenced by human activity except in rare instances and an annual productive season compressed into a few months. In addition, consistently low ambient DIN ensures that ecologically meaningful data

can be secured.

Finally, study in an arctic lake offers a unique opportunity to extend observations of known physical influences on phytoplankton DIN utilization to extremes characteristic of high latitudes. Algae are exposed to continuous daylight and persistently cold water during the brief arctic summer.

Site Description

Toolik Lake (68°38′N;149°38′W) is located at an elevation of 720 m on the northern flanks of Alaska's Brooks Range (Fig. 1-1). Access is via the Dalton Highway, a gravel road linking Fairbanks to Prudhoe Bay along the Trans-Alaska Pipeline Corridor. The drainage is composed of glacial till and outwash deposited by retreat of the Itkillik II glaciation about 12,000-14,000 yr B.P. (Hamilton and Porter 1975). Tussock and upland heath tundra dominate the vegetation and provide nearly 100% ground cover. Permafrost with a maximum thaw depth of 0.5 m (K. Kielland, Inst. Arctic Biol., Univ. AK, pers. comm.) underlies the entire area. Soils are highly organic, poorly drained and consist mostly of silt loams and silty clays with an overlying peat surface (Brown and Berg 1980). Annually, the air temperature averages -10°C and precipitation totals 20 cm, divided equally between rain and snow (Brown and Berg 1980).

The Toolik watershed covers 65 km^2 and the lake surface 1.5, giving a ratio of 43 for catchment/lake surface. The main inlet

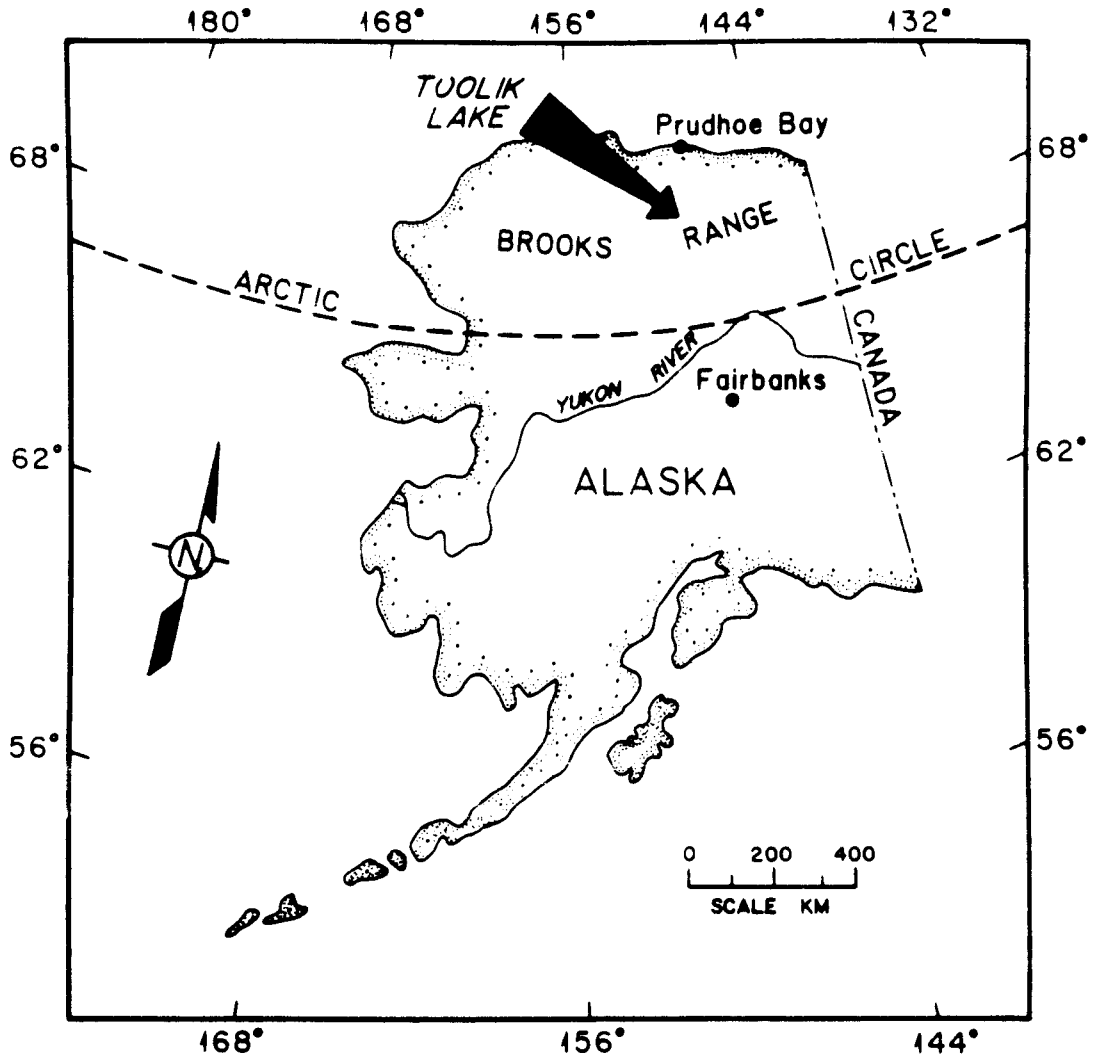

Fig. 1-1. Location map, Toolik Lake.

stream (Fig. 1-2; Inlet 1) drains about 75% of the watershed, including twelve small lakes above Toolik. A secondary inlet (Inlet 2) and ephemeral rivulets on the lake's west side drain the balance. A single outlet is on the north side of the lake. Flow commences in these major streams during mid-May and ceases in mid-September. Lake water renewal time is 0.5-1.0 yr.

Owing to irregular melting of glacial ice, Toolik is divided into five basins separated by rocky shoals (Fig. 1-2). Maximum and mean depths are 25 and 7 m and the total volume is 10.6×10^6 m^3. Cobbles and boulders dominate the littoral zone to about 2.5 m. These grade into silty sediments which show irregular patches of *Nitella* sp. and aquatic mosses to about 6 m.

The ice-free period in the lake is brief (late June until late September), but thermal stratification develops for 5-6 wk during July and August. Maximum depth of the thermocline is 8-10 m, with temperatures at the lake surface and bottom reaching 16 and 7°C. Bottom waters are oxic year-round (Cornwell 1983 and unpublished data). Lake water is a calcium bicarbonate type with a total alkalinity of about 0.4 mequiv·L^{-1}. Nutrient concentrations are persistently low during the ice-free season. Soluble reactive phosphorus is undetectable (<0.03 μmol·L^{-1}) and total dissolved phosphorus averages 0.11 (Cornwell 1983 and unpublished data), while NO_3^- and NH_4^+ average 0.10 and 0.17.

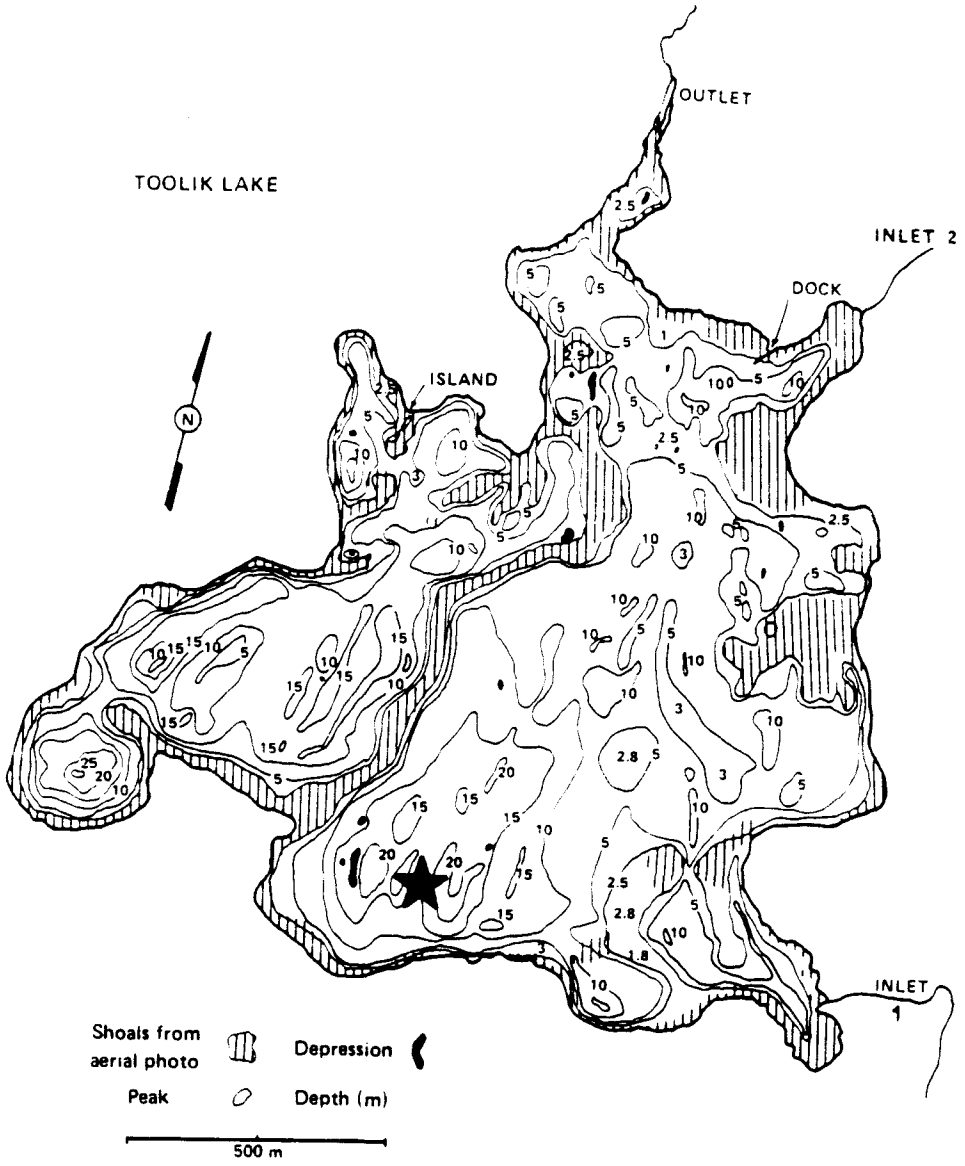

Fig. 1-2. Bathymetric map of Toolik Lake showing major inlets, outlet and permanent lake sampling site (★). Contours redrawn from J. Miller (Dept. Zoology, N. Carolina State Univ., unpublished data).

Dissertation Organization

Chapter 2 describes methods used throughout the entire study and gives the accuracy and precision of routine biological and chemical measurements. Chapters 3-7 address Components 1-5, respectively. Each of these chapters consists of an Introduction detailing the background, justification and goals of that component, a Methods section outlining unique procedures and lastly, Results and Discussion. Chapter 8, similar in format, focuses on Component 6 and ties the previously presented data into a summary. Appendices A-G contain the raw data corresponding to Chapters 2-8.

CHAPTER 2. METHODS

Unless noted otherwise, sample collection and analysis were performed by the author.

All lake samples were collected in 1979 to 1982 from a permanently established, deepwater station in the main lake basin (Fig. 1-2) while stream samples were obtained from variable (depending on volume of flow) locations within 50 m of the lake. Lentic and lotic samples were collected with an underwater pump and by directly submersing rinsed 4-L polyethylene bottles into the main flow, respectively. J.C. Cornwell (Inst. Mar. Sci., Univ. AK) assisted in water collection during 1980.

Physical

All determinations of lake water temperature were made by immersing a hand-held thermometer in the pump outflow. The attenuation of photosynthetically active radiation (PAR) through the water column was determined using a Lambda quantum meter (LI 185) and underwater sensor (LI 192S). Extinction coefficients were calculated according to Golterman et al. (1978). Incident PAR was determined with a shoreside Lambda quantum sensor (LI 190S) and recorded with a digital integrator (LI 500).

Chemical

Single total alkalinity determinations were made potentiometrically on whole water samples (Golterman et al. 1978) by

titrating with 0.01 N HCl to a theoretical bicarbonate endpoint of pH 4.8 (Barnes 1964).

Samples for other routine chemical analyses were filtered through preignited (defined here as 6 h at 450°C) Gelman A/E glass fiber filters, with filters and filtrate stored frozen for later analysis. For the filtrate, single determinations of NO_3^- (NO_3^-+NO_2^-) and NH_4^+ followed automated Cu-Cd reduction and phenolhypochlorite methods (Whitledge et al. 1981), while single DON determinations were by persulfate oxidation (Solórzano and Sharp 1980). Duplicate particulate nitrogen (PN) determinations on filter-trapped seston were also made by persulfate oxidation (Solórzano and Sharp 1980), except where noted. All DIN analyses were performed by K. Krogslund (Dept. Ocn., Univ. WA).

Biological

Duplicate chlorophyll a (Chl a) determinations were made by fluorometric analysis of acidified and unacidified acetone extracts of seston trapped on preignited Gelman A/E glass fiber filters (Strickland and Parsons 1972).

All biological samples were prescreened through 202-μm Nitex mesh to remove large zooplankton prior to experimental manipulation. Pump-collected samples showed activity in terms of ^{14}C, $^{15}NO_3^-$ and $^{15}NH_4^+$ uptake not significantly different from more traditional Van Dorn-collected samples at the same depth (Student's t-test; df=18, all cases; P=0.41-0.80). Clear 1.3 or 2.4-L

polystyrene containers were used in experiments assessing DIN utilization while 0.165-L borosilicate glass bottles were employed when measuring DIC uptake. Radiocarbon additions ($NaH^{14}CO_3$) were at an activity of 315-575 $kBq \cdot L^{-1}$, while ^{15}N additions (99 atom-% $Na^{15}NO_3$ or $^{15}NH_4Cl$) were made at a level expected to approximately saturate the phytoplankton uptake capacity (3.07-4.82 $\mu mol \cdot L^{-1}$). An exception involved kinetic experiments where $DI^{15}N$ was added serially in eight concentrations ranging from 0.1-3.07 $\mu mol \cdot L^{-1}$. All $^{15}NO_3^-$ and $^{15}NH_4^+$ uptake determinations were made in duplicate or triplicate while a single opaque and 3 or 4 clear bottles were used to assess $DI^{14}C$ utilization for each depth or treatment, depending on experimental design.

All experiments were terminated by immediate low vacuum (<20 cm Hg) filtration of the entire contents of each sample vessel onto an uncombusted (^{14}C) or preignited (^{15}N) Gelman A/E glass fiber filter. Use of Gelman A/E filters as opposed to 0.45-μm nitrocellulose filters usually employed for ^{14}C experiments ensured that a consistent size fraction of the plankton was always sampled with respect to ^{14}C and ^{15}N utilization. A single comparison of mean ^{14}C activity retained by each filter type showed that for a surface water sample Gelman trapped significantly more labeled particulates than Millipore (Student's t-test; df=18, $P<0.01$).

Seston-containing filters were rinsed with 25-50 mL filtered lake water, air-dried (^{14}C) or frozen and subsequently dried at 60°C (^{15}N). The ^{15}N content of filter-trapped particulates was

measured in a Bendix Model 17-210 mass spectrometer using a modified Dumas technique (Fiedler and Proksch 1975). Beta activity (^{14}C) was determined by liquid scintillation spectrometry (Beckman LS100C instrument) following immersion of filters in 5 mL of Aquasol-2 cocktail.

Generally, DIC and DIN utilization rates are expressed here as ρ, the absolute or biological transport rate, with units of nmol substrate utilized per volume per time. When data are best presented in biomass-independent manner I give V ($= \rho \cdot PN^{-1}$), the element-specific uptake rate with units of reciprocal time or $\rho \cdot Chl^{-1}$, the chlorophyll-specific transport rate with units of nmol substrate utilized per μg Chl *a* per time.

Values of $\rho(C)$ were calculated as the difference between quench-corrected (channel ratio technique) light and dark bottle estimates times an isotope discrimination factor of 1.06 (Vollenweider 1974). Available ^{12}C was determined from alkalinity, pH and temperature measurements following Golterman et al. (1978).

Directly determined DIN transport rates were at or near maximal owing to the quantity of ^{15}N added. Because amended ^{15}N increased ambient N (^{14}N) of the same form by a factor of 20-30, these rates are considered to be "measured-enhanced" (MacIsaac and Dugdale 1972). The rate of NO_3^- or NH_4^+ transport can often be related to its extracellular concentration (S) by the Michaelis-Menten relationship (MacIsaac and Dugdale 1972):

$$\rho = \rho_m \frac{S}{K_t + S} \quad (2\text{-}1)$$

where K_t (half-saturation constant) is the substrate concentration necessary to achieve half the maximum transport rate, ρ_m. Equation 2-1 was directly fitted to kinetic experiment data for NO_3^- and NH_4^+ by a least squares routine (Cleland 1967) and K_t evaluated. If estimates of ambient transport rates were needed, the value of K_t obtained closest to the date of interest was used in conjunction with the measured-enhanced transport rate (ρ) and nutrient concentration at which it was made (S = ambient ^{14}N plus added ^{15}N) to calculate ρ_m from Equation 2-1. The *in situ* value of ρ was then computed by substituting ρ_m, K_t and the ambient nutrient level (S) into Equation 2-1. Note that specific rates of activity (V, $\rho \cdot Chl^{-1}$) can replace ρ in Equation 2-1 and K_t is unaffected.

Accuracy, Precision and Statistics

Following Sutcliffe (1979), the lower limit of detection for the mass spectrometer was calculated as 0.15 atom-% excess. For ^{15}N-amended samples, atom-% excess in the particulate fraction ranged from 0.1-11.3. The few that fell below 0.15 were discarded as indistinguishable from the natural abundance. The majority of samples were enriched by 1-7 atom-%, where the mass spectrometer showed a relative error of <3% and a coefficient of variation (CV = standard deviation divided by sample mean, expressed as %) among

replicate samples of ≤4% (Table 2-1).

Analyses for NO_3^- and NH_4^+ showed the least precision of routine chemical measurements (Table 2-2), as concentrations sometimes approached the lower detection limit (0.03 $\mu mol \cdot L^{-1}$; McCarthy 1980). These data are somewhat higher than CVs given by Whitledge et al. (1981) for automated NO_3^- (11%) and NH_4^+ (9%) determinations at a level of 0.09 $\mu mol \cdot L^{-1}$. However, my data represent the worst possible case for Toolik. Ambient nutrients were somewhat lower than usual, each sample was individually collected in a separate bottle and these were randomly dispersed among samples collected through the entire season to avoid all ten replicates being run consecutively. Biological measurements showed surprisingly good precision as CVs ranged from 3-13%. Patchiness often leads to CVs of >20% for such samples (Stainton et al. 1977).

Common statistical analyses used here follow Sokal and Rohlf (1969). Unless stated otherwise, values of $P<0.05$ were considered significant. Finally, whenever means are reported, the associated value represents one standard deviation ($\bar{x} \pm SD$).

Table 2-1. Accuracy and precision of Bendix Model 17-210 mass spectrometer as determined by repeated measurements of atom-% ^{15}N in reagent grade NH_4Cl (natural abundance 0.37 atom-%) and C_6H_4-CONHCO of known atom-% ^{15}N.

Compound	Level (atom-% ^{15}N)	Number of determinations (n)	Measured mean atom-% ^{15}N ($\bar{X}$)	Accuracy as relative error (%)	Precision as coefficient of variation (%)
NH_4Cl	0.37	6	0.36	-2.7	8.6
C_6H_4-CONHCO	1.02	3	1.03	1.0	3.8
	4.00	3	3.89	-2.8	1.0
	7.00	3	6.99	-0.1	4.0
	10.02	3	9.79	-2.2	3.7
	15.03	3	14.22	-5.4	1.3
	25.03	3	22.24	-11.1	3.7

Table 2-2. Estimates for precision (as coefficients of variation) of routine chemical and biological measurements in Toolik Lake at typical concentrations or levels of activity.

Analysis	Level	Coefficient of variation (%)
Chlorophyll a	0.5-3.1 $\mu g \cdot L^{-1}$	3[a]
Particulate-N	1.2-4.1 $\mu mol \cdot L^{-1}$	7[a]
Nitrate-N	0.05-0.07 $\mu mol \cdot L^{-1}$	19[b]
Ammonium-N	0.04-0.14 $\mu mol \cdot L^{-1}$	15[b]
Dissolved organic-N	17.1 $\mu mol \cdot L^{-1}$	2[c]
Dissolved inorganic-C transport rate	830-5250 $nmol \cdot L^{-1} \cdot d^{-1}$	5[a]
Nitrate transport rate	3-48 $nmol \cdot L^{-1} \cdot d^{-1}$	12[a]
Ammonium transport rate	33-156 $nmol \cdot L^{-1} \cdot d^{-1}$	13[a]

[a]Average for 20 replicate (C transport rate) or duplicate (all other analyses) samples collected from 1 m at ca. 10 d intervals during 100 d field seasons in 1980 and 1981.

[b]Average for 10 samples collected from 1 m on a single date during each year, 1980 and 1981.

[c]Average for 10 samples collected from 1 m on a single date in 1980.

CHAPTER 3. NITROGEN MASS BALANCE

Introduction

Specific aims of this component were to: (a) determine major seasonal fluxes of N to and from Toolik, and thereby evaluate supply and loss terms to the phytoplankton, (b) examine the influence of watershed-stream interactions on allochthonous N input to the lake and (c) characterize Toolik and its inflowing and outflowing waters with regard to seasonal changes in nitrogenous nutrients. This aspect of the study was essential from the standpoint that a meaningful assessment of phytoplankton-nitrogen interactions must include a mass balance for this nutrient.

Aside from my need, these data provide useful baseline information for determining the potential impact of oil, mineral and tourist industry development on the North Slope. Previously, nutrient budgets for arctic waters have been prepared only for Char (Schindler et al. 1974a; de March 1975) and Meretta (Schindler et al. 1974b) lakes in Canada and for shallow thaw ponds near Barrow, Alaska (Prentki et al. 1980).

Methods

Due to logistic problems, it was impossible to assess all features of the N cycle during each study year. My most comprehensive stream flow and lake productivity data are for 1980, so I have developed an elemental budget for that year utilizing corroborative data from 1979 and 1981 where appropriate.

Unless noted, stream and lake measurements were made from 13 May (the day stream flow commenced) through 31 August 1980. Lake profiles for nitrogenous nutrients were obtained at about 10 d intervals while Inlet 1 and Outlet (Fig. 1-2) were sampled daily during initial flow and approximately weekly thereafter, as well as during episodic storm events. Concurrently, midwater flow determinations were made with a Gurley meter at 1-m intervals in a cross-stream transect. Inlet 2 was sampled whenever flow was sufficient for accurate gauging. Stream discharge was calculated by J.C. Cornwell as the product of current velocity and cross-sectional area.

Precipitation chemistry was determined on samples collected in polyethylene pans, but no volume determinations were made.

The daily flux of DIN to the particulate fraction (phytoplankton) was calculated from lake profiles of DIN transport taken at ca. 10 d intervals in 1980 and 1981 according to methods described in Chapter 6. Data were time- and depth-integrated to calculate areal $DI^{15}N$ transport for the 1980 and 1981 sampling seasons.

The loss of PN from the trophogenic zone was calculated as material captured in two acrylic sediment traps (aspect ratio 2.9) moored approximately 100 m apart at a depth of 16 m. Traps were deployed and recovered every 3-9 d during June through August 1981 following the methodology of Kirchner (1975). The PN content of sedimenting seston (between trap CV = 11%) was measured using a Perkin Elmer 240C Elemental Analyzer after homogenization and fil-

tration onto preignited Gelman A/E glass fiber filters.

The long-term average rate of permanent N accumulation in the sediment was determined by ^{210}Pb dating and the historic rate of microbial decomposition of settled organic matter by sediment total nitrogen (TN) profiles. Samples were collected and analyzed by J.C. Cornwell according to previously described techniques (Cornwell 1983). In addition, the DIN flux from the sediment was calculated as the volume-weighted, overwinter (15 September 1979 to 20 May 1980) accumulation per m^2 lake surface, assuming stream flow and phytoplankton activity were negligible. I have noted that inlet and outlet streams for Toolik freeze solidly around mid-September while observations for other arctic lakes (Hobbie 1964; Howard and Prescott 1971; Kalff and Welch 1974) show that nearly all of the annual phytoplankton primary production occurs during May through September.

Results and Discussion

The shallow active layer of the watershed led to rapid variations in dicharge rates for inlet streams during runoff and major storms (Fig. 3-1). The short water renewal time (Table 3-1) guaranteed an equally dramatic response at Outlet (Fig. 3-1). For 1980, Inlets 1 and 2 provided 71 and 9% of surface water discharge to Toolik with diffuse sources accounting for the remaining 20%. Unpublished National Weather Service (NWS) data for a site 15 km to the south from September 1979 through August 1980 showed a total

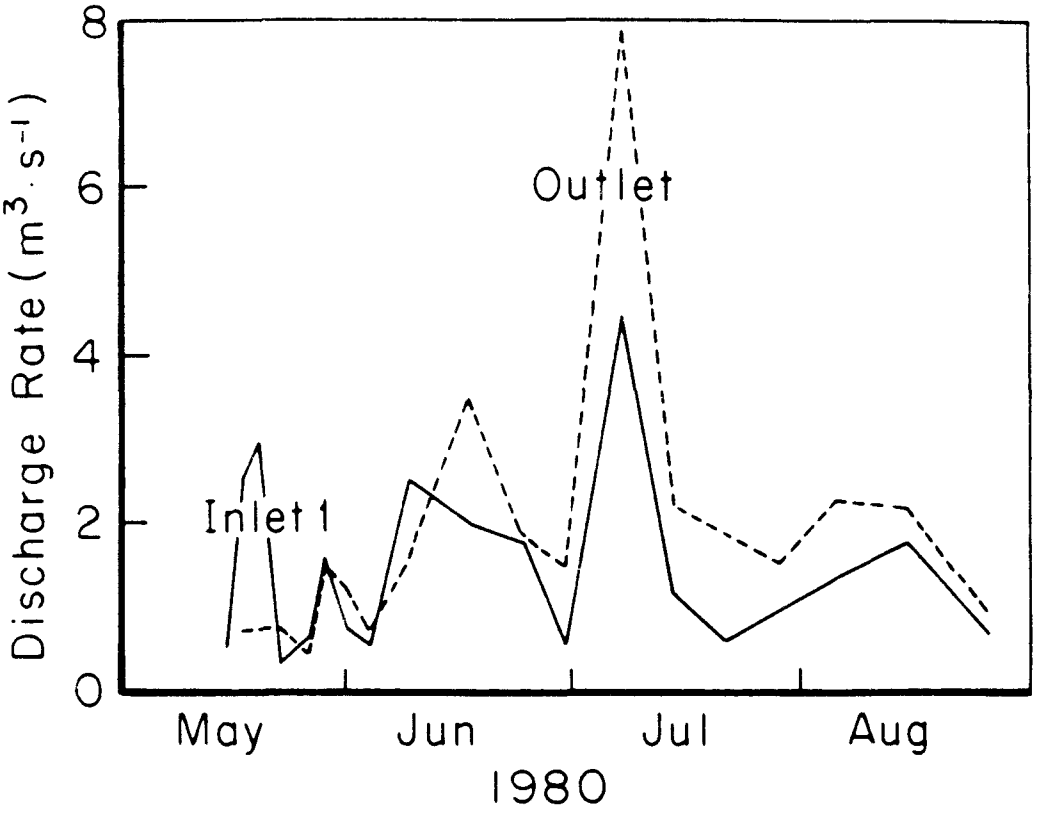

Fig. 3-1. Temporal variations in water discharge rates at Inlet 1 and Outlet, Toolik Lake.

Table 3-1. Summary of stream flows to and from Toolik Lake during 1980. Undefined inflow represents input from ephemeral and ungauged streams and was calculated as the difference between measured outflow and inflows assuming lake stage remained constant and evaporation and input from precipitation were negligible.

	Inflow volume (millions of m^3)	Water level change (m)
Inlet 1	13.7	9.19
Inlet 2	1.7	1.14
Undefined inflow	4.0	2.68
Total inflow	19.4	13.02
Outlet	19.4	13.02
Water renewal time (yr)	0.5	
Sampling season	13 May - 31 August	

precipitation of 30 cm (including my linear interpolation between months to estimate missing April and July data), while evaporative water loss from the lake was estimated to be about 15 cm based on data from Brown et al. (1968), Dingman et al. (1980) and Miller et al. (1980). Comparing these values with the 13 m equivalent of stream-induced water level change in the lake (Table 3-1), it is clear that the annual hydrologic regime was dominated by lotic fluxes.

For the lake ecosystem, concentrations of all nitrogenous nutrients except NO_3^- showed the widest range at Inlet 1 (Table 3-2). Reduced ranges for the lake and Outlet undoubtedly reflect the moderating influence of storage. Nonetheless, the water renewal time of only 0.5 yr ensured that means for all N species were fairly similar for lotic and lentic components. Moreover, the data indicate ecosystem dominance by DON, as levels averaged roughly 10 and 40 times greater than PN and DIN. Concentrations of all forms of N in precipitation also showed marked variability (Table 3-2). In general, levels of DIN were higher and DON lower than in surface waters.

The most striking aspect of lake water profiles for nitrogenous nutrients was the elevated under-ice NO_3^- (Fig. 3-2A), presumably from nitrification in the sediment and release to the water column during the winter period of reduced phytoplankton activity (Klingensmith and Alexander 1983). A nutricline developed by late May from flux to the phytoplankton and dilution of the lake

Table 3-2. Comparison of ranges and mean values ($\mu mol \cdot L^{-1}$) of several chemical characteristics of Toolik Lake, Inlet 1, Outlet and direct precipitation (snow and rain) during 1980.

Parameter	Toolik Lake	Inlet 1	Outlet	Precipitation
NO_3^--N	0-3.33	0-0.91	0-1.02	0.26-6.62
	0.46[a]	0.30	0.24	1.74
NH_4^+-N	0-0.28	0.08-0.67	0.08-0.28	0.03-2.71
	0.17	0.26	0.18	0.74
Dissolved organic-N	11-30	14-40	12-27	3.5-10.4
	17	21	17	6.3
Particulate-N	0.6-6.0	1.1-5.8	2.0-4.2	-
	2.1	2.6	3.0	

[a]Mean during open water period = 0.10 $\mu mol \cdot L^{-1}$ (see text for details).

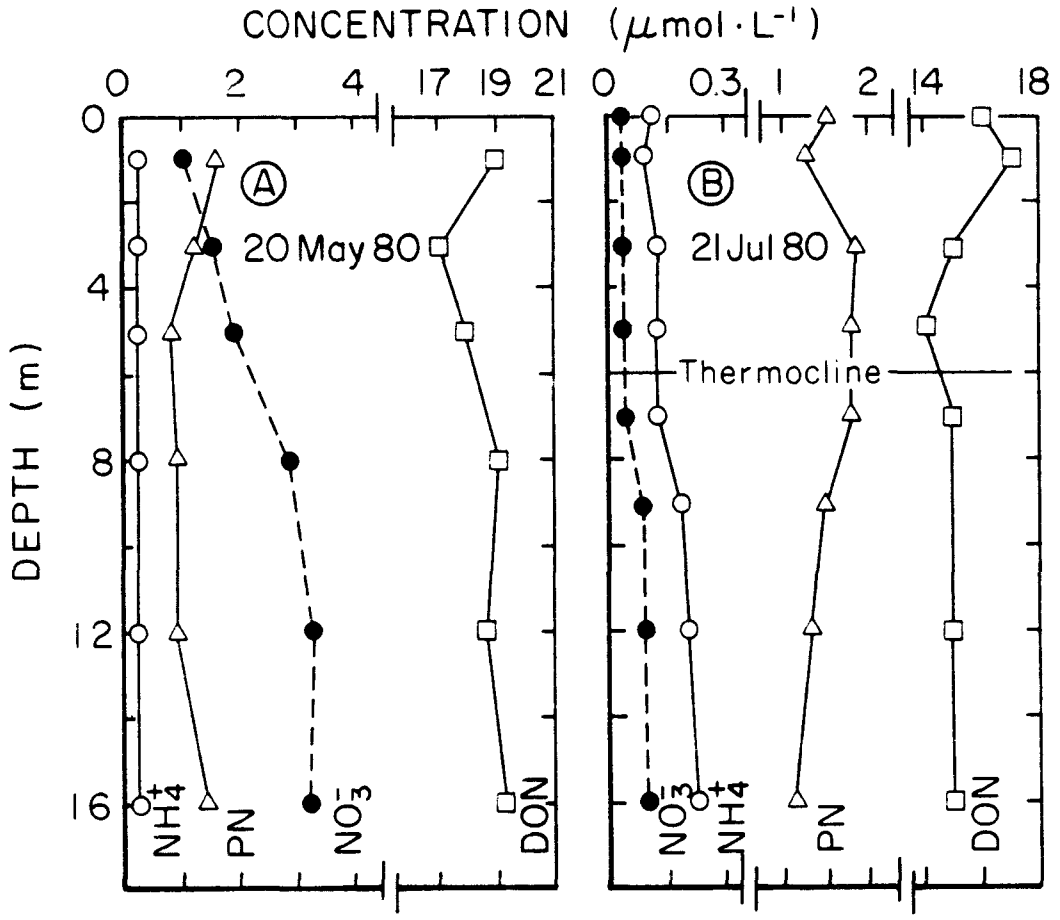

Fig. 3-2. Typical (A) spring and (B) summer profiles of nitrogenous nutrients, Toolik Lake. PN, particulate nitrogen; DON, dissolved organic nitrogen.

surface with melt water (not shown). This situation persisted to early June when NO_3^- returned to homogeneously low levels. For the period of study, other N species were characterized by temporally and spatially constant concentrations, even during thermal stratification (Fig. 3-2B).

Stream water levels of all forms of N were high at the initiation of flow in mid-May, decreasing to mid-June as runoff diminished (Fig. 3-3A,B). Thereafter, concentrations remained relatively invariant at Outlet, but fluctuated considerably for DIN (NO_3^- highly variable; NH_4^+ constant) at Inlet 1 (cf. Fig. 3-1, Fig. 3-3A). This apparently reflected input from increased nitrification with warming soils in the watershed (Gersper et al. 1980) and subsequent storm-induced leaching (cf. Fig. 3-1, Fig. 3-3A).

The riverine flux of N to the lake was calculated as the product of discharge (Inlets 1 and 2) times the nutrient concentration therein, summed for the period of record and normalized to 1 m^2 lake surface. Input from undefined sources (Table 3-1) was computed as the product of water volume necessary to complete the hydrologic balance times the discharge-weighted mean nutrient level of Inlets 1 and 2. The efficacy of this approach was tested by monitoring the conservative cation Na^+; agreement to about 3% was found between Na^+ loads of the outflow and summed inflows. J.C. Cornwell developed the computer routine used to generate these data and peformed the Na^+ analyses. Nitrogen loading via direct precipitation was calculated from unpublished NWS data for volume

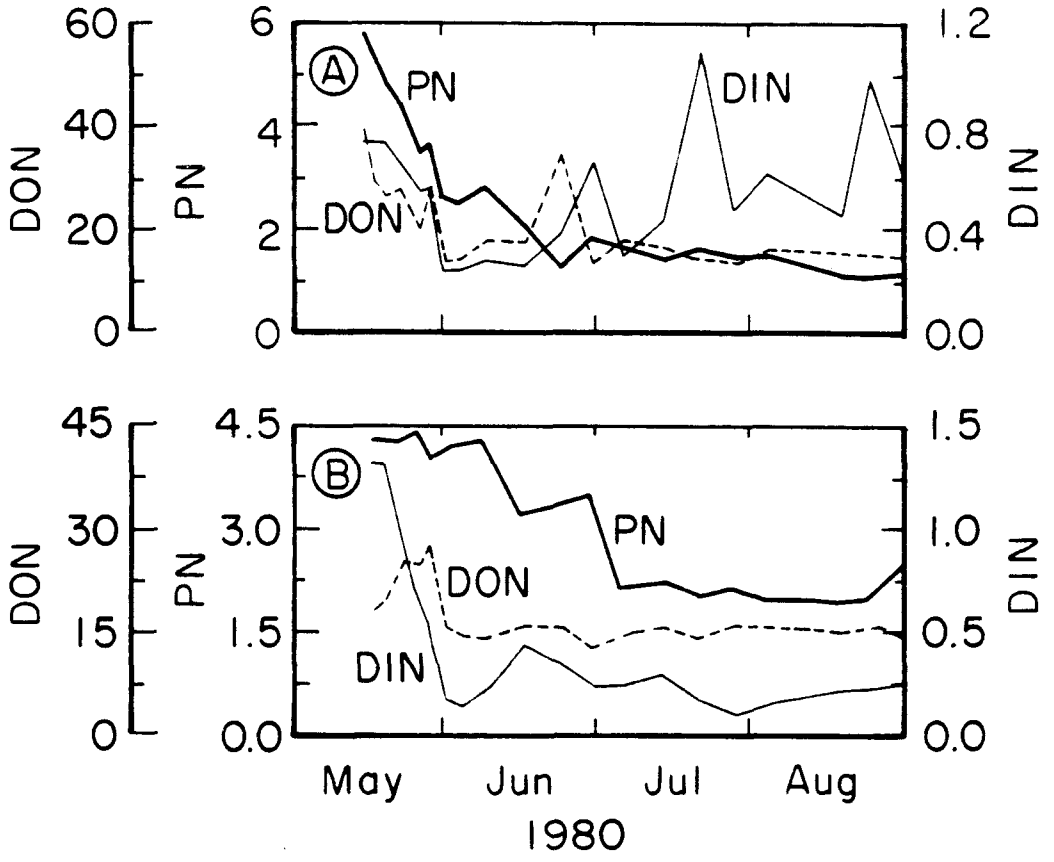

Fig. 3-3. Temporal variations in concentrations ($\mu mol \cdot L^{-1}$) of nitrogenous nutrients at (A) Inlet 1 and (B) Outlet, Toolik Lake. DIN, dissolved inorganic nitrogen; PN, particulate nitrogen; DON, dissolved organic nitrogen.

and measured concentrations from Table 3-2.

The allochthonous nutrient load to the lake was controlled by riverine fluxes as direct precipitation supplied only about 2% of the annual TN flux (Table 3-3). Dissolved organic-N constituted 87% of the TN delivered. The lake acted as a TN sink, retaining 18% of the allochthonous input, predominately at the expense of DON.

The TN export rate from the Inlet 1 watershed during 1980 was 305 kmol, based on the known flux from Inlet 1 to Toolik and the watershed area derived from topographic maps. Input to the watershed from precipitation totalled 308 kmol TN, giving an apparent retention efficiency of about 1%. However, import from N-fixation was not determined and may amount to 75% of the TN input per annum to the tundra (Barsdate and Alexander 1975).

During June through August 1981, the DIN flux to the phytoplankton (PN) totalled 67 $mmol \cdot m^{-2}$, while the PN loss from the trophogenic zone was 40 and the gross allochthonous PN input was 17. Hence, the PN flux from the trophogenic zone tracked phytoplankton transport of DIN only marginally (Fig. 3-4).

Assuming the riverine input was refractory and totally sedimented, or alternatively, completely mineralized in the water column, 34-60% of the $DI^{15}N$ primary production sedimented and 40-66% was recycled. Extrapolating these data to an annual basis (productive season taken here to be same as period of stream flow, mid-May through mid-September) gives a loss rate from the

Table 3-3. Approximate annual loading rates ($mmol \cdot m^{-2}$ lake surface) for nitrogenous nutrients in Toolik Lake. Stream inputs and outputs were measured from 13 May through 31 August 1980 and do not include ca. 2 wk of low volume flow to mid-September. Estimates of input from direct precipitation encompass 15 September 1979 through 15 September 1980.

Parameter	Total stream inflow	Direct precipitation	Total input	Stream outflow	Net (in-out)	% input retained
Dissolved inorganic-N	5.9	0.7	6.6	3.5	3.1	47
Dissolved organic-N	249	2.0[a]	251	201	50	20
Particulate-N	28.4	3.6[b]	32.0	33.4	-1.4	-4
Total-N	283.3	6.3	290	238	52	18
Na^+	247	-		255	-8	-3

[a]Estimate assumes equal concentrations of dissolved organic N in rain and snow.

[b]Estimate derived from concentration in bulk precipitation at Char Lake (de March 1975).

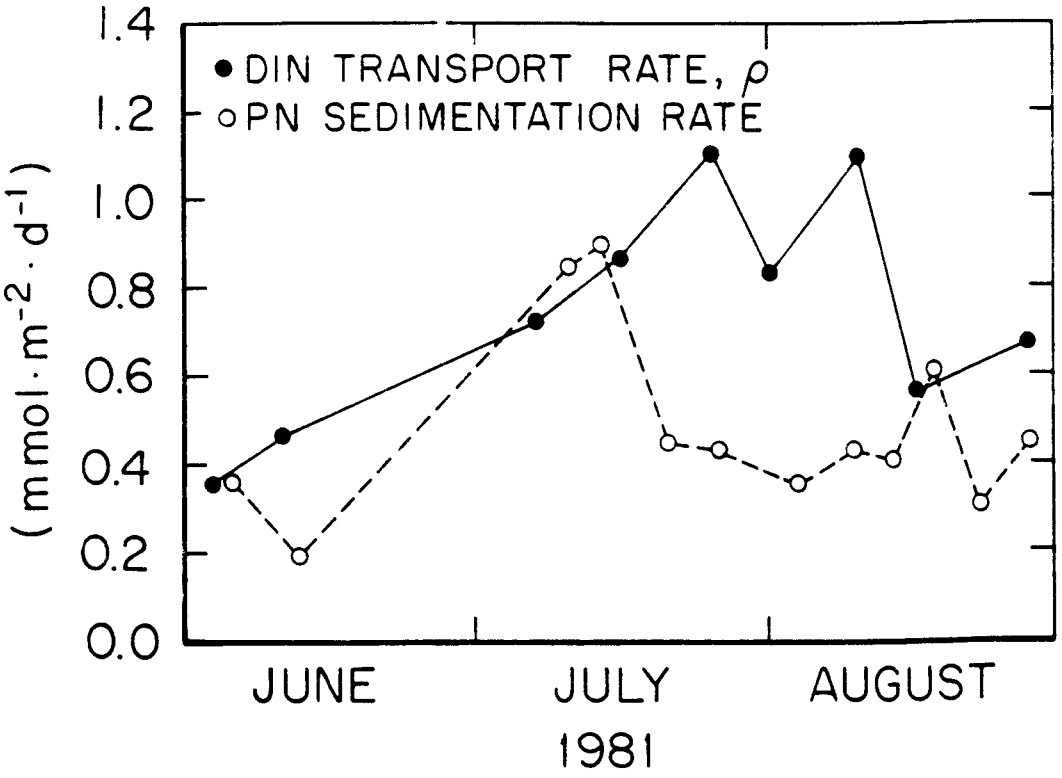

Fig. 3-4. Seasonal patterns of dissolved inorganic nitrogen (DIN) transport by phytoplankton and flux of particulate nitrogen (PN) to sediment traps, Toolik Lake.

trophogenic zone of 41-50 $mmol \cdot m^{-2}$ with the following assumptions: (a) the proportion of $DI^{15}N$ primary production that occurred early (15-31 May) and late (1-15 September) in the growing season was constant for 1979 through 1981 and 34-60% of this unmeasured biosynthesis left the trophogenic zone, (b) the measured riverine input of PN to the lake for 1981 was 70% of the annual total and (c) the unquantified PN influx from streams totally sedimented.

The ^{210}Pb-derived rate of PN sedimentation was 21 $mmol \cdot m^{-2} \cdot yr^{-1}$, or 42-51% of the rate estimated from sediment trap data. The difference arises from mineralization of organic matter at the sediment-water interface and the fact that the ^{210}Pb estimate is time-averaged.

Vertical profiles for sediment TN indicate that 55% of originally deposited material had mineralized. In conjunction with ^{210}Pb data, this gives a historic rate of release of DIN from the sediment of 11.5 $mmol \cdot m^{-2} \cdot yr^{-1}$. In contrast, the annual rate calculated from the overwinter accumulation of DIN in the lake water was 22.2 $mmol \cdot m^{-2}$.

The nitrogen budget for Toolik (Fig. 3-5) shows no serious inconsistencies in estimates of dominant flux terms. The water column and sediment mass balances agree to within 11 and 5-42%. I accept a greater error in the latter because of differences in intrinsic time scales associated with some flux measurements.

Toolik data corroborate well that for Char Lake (Schindler et al. 1974a; de March 1975, 1978) in that lake water DIN was consis-

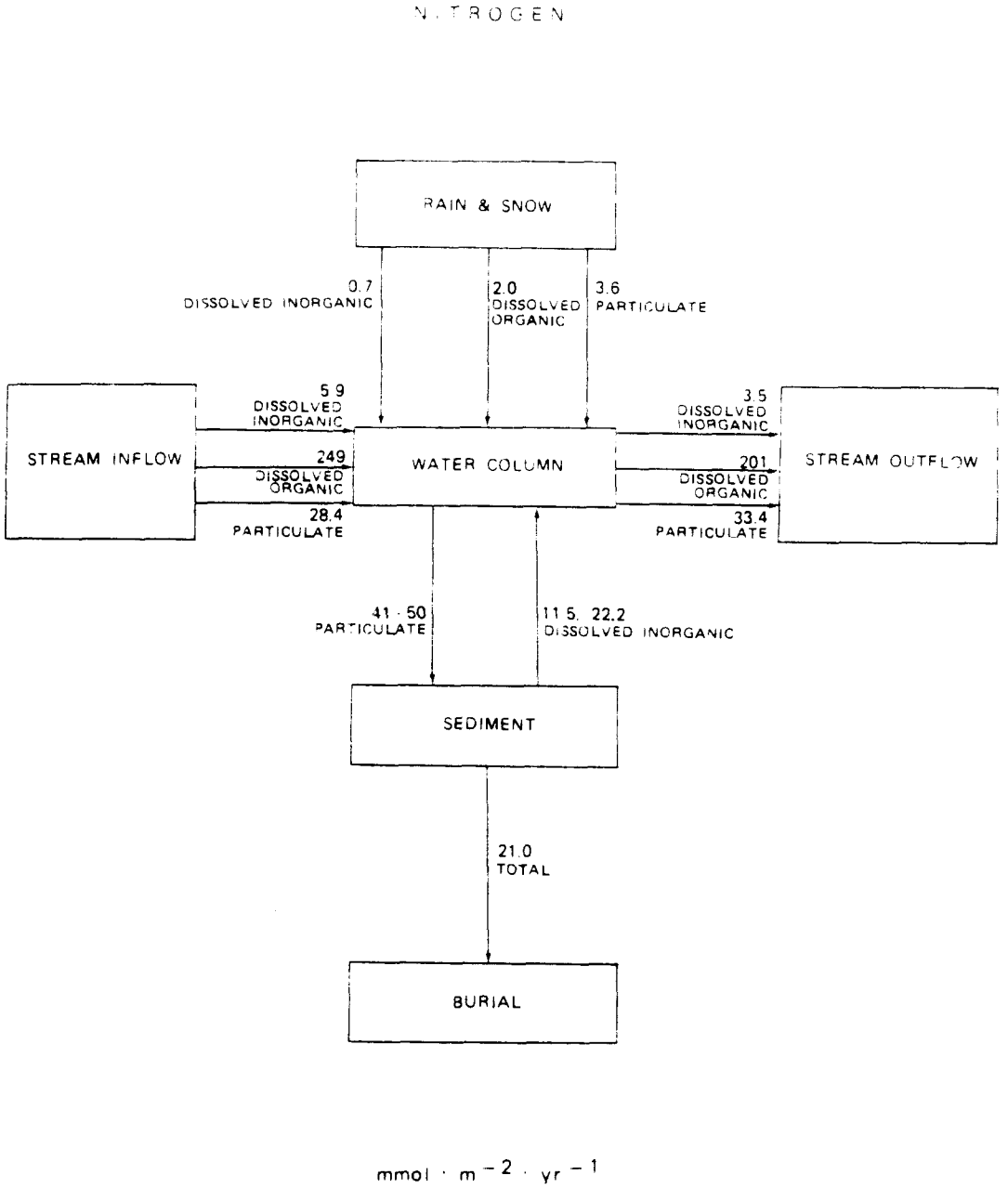

Fig. 3-5. Toolik Lake nitrogen cycle. All fluxes normalized to 1 m^2 lake surface.

tently low except for ephemerally elevated spring NO_3^- and that bulk precipitation contributed little to the annual N budget. There were several differences, however, attributable to the larger ratio of catchment to lake surface, greater percent plant cover in the drainage and shorter water renewal time for Toolik (8:1, 5-7% and 9-14 yr, respectively for Char). These included a higher allochthonous loading rate, percent retention of input, watershed export rate and permanent sedimentation rate for N in Toolik, by factors of 13, 3, 3 and 3. Overall, the data point to a relatively simple, nutrient-impoverished ecosystem where nitrogenous nutrient pathways are few and the magnitude of flux terms among the smallest recorded.

CHAPTER 4. INFLUENCES OF TEMPERATURE AND LIGHT ON PHYTOPLANKTON TRANSPORT OF DIN

Introduction

Continuous culture studies emphasize the potential influence of the physical variables light and temperature on phytoplankton growth (reviewed by Rhee 1982). For photoautotrophs, light serves as an energy source (Yentsch 1980) while temperature affects physiological processes including respiration, membrane permeability and macromolecular synthesis (Morita 1975). For example, early studies in batch cultures of *Anabaena cylindrica* showed that, within reason, increases in light accelerated NO_3^- assimilation (Hattori 1962) while increases in temperature gave enhanced rates of N-fixation (Fogg and Than-Tun 1960).

Field ecologists have directed only moderate effort toward extending such observations to *in situ* DIN utilization. The influence of light on DIN uptake (transport) has received the most attention because trophogenic waters can be partitioned into upper and lower regions where nutrients and light, respectively, regulate autotrophic production if the euphotic depth exceeds the mixed layer depth. In contrast, the relationship between temperature and algal DIN uptake has been largely overlooked. This may be due to the relatively moderate seasonal changes in temperature for marine waters (Sournia 1974) and the conviction that temperature-controlled growth is seldom achieved owing to the predominance of other influencing factors, notably suboptimal nutrients (Eppley

1972).

In suboptimal light or temperature, growth regulation for nutrient-stressed algae has been shown to be some nonmultiplicative yet nonadditive function of nutrient concentration and physical conditions (Rhee and Gotham 1981a,b). Although undocumented, the case for nutrient uptake in oligotrophic waters may be equally complex. Consequently, Falkowski (1977) suggested that bisubstrate (ambient nutrient level and light) kinetics may best describe NO_3^- uptake in this situation.

For my experiments, such complications have been avoided by adding sufficient $DI^{15}N$ to saturate the phytoplankton transport capacity. That is, NO_3^- or NH_4^+ was in excess (>3 $\mu mol \cdot L^{-1}$; determined from kinetic studies performed concurrently and described in Chapters 6 and 7) when measuring respective rates of transport. This has the advantage of isolating the individual effects of suboptimal temperature or light on N-saturated (maximum) rates of DIN transport, but allows only qualitative assessment of these physical influences at ambient nutrient levels.

Specific aims of this facet of the study were to: (a) describe quantitatively changes in maximum DIN transport by phytoplankton with variations in water temperature, (b) relate seasonal shifts in the optimum temperature for N-saturated transport (T_{opt}) to the ambient water temperature (T_{amb}), i.e. determine whether there was a seasonal adaptation or succession of the indigenous population to maintain a close coupling between T_{opt} and

T_{amb}, (c) test for a light dependence in maximum rates of DIN transport by phytoplankton exposed naturally to a continuous but fluctuating photoperiod, (d) calculate half-saturation constants for light intensity in maximum DIN transport when a light dependence was evident, and (e) use results to predict the influences of light and temperature on DIN transport at *in situ* lake levels of nutrient.

Methods

In four temperature dependence experiments (coded consecutively T1-T4), mid-epilimnetic water (3 m; ca. 10-15% surface light penetration) was collected at local midnight into 30 sample bottles. At lakeside, aquarium heaters and cryocool units maintained five 1-m^3, water-filled incubators at constant temperatures ranging from 3-29°C. One incubator was always held at T_{amb} by continual exchange of 2 m lake water via a submersible pump. Over an 8 h acclimation period, bottles were systematically stepped from T_{amb} up or down the temperature range of the incubators until each held six. Half the bottles in each incubator were then enriched with transport-saturating $^{15}NO_3^-$ and the other half with transport-saturating $^{15}NH_4^+$. DI^{15}N transport was measured for 8 h. Incubators were screened throughout the periods of acclimation and transport to allow 50% transmittance of surface irradiance.

Nine light dependence experiments (coded consecutively LT1-LT9) were begun around 0800 local time. Transport-saturating

$^{15}NO_3^-$ or $^{15}NH_4^+$ was added to mid-epilimnetic water collected into clear and opaque bottles, as well as to containers covered with neutral density screens (Perforated Products Inc. No. 15G, 10/40, 40P, 15S, 4T and 50W allowing ca. 48, 25, 12, 9, 7 and 1% light transmission, respectively). For each $DI^{15}N$ species, duplicate bottles of each simulated light level were suspended horizontally at 0.25 m in the lake for 24 h. During incubation PAR was continuously measured at 0.25 m.

Results and Discussion

A. Temperature Dependence Experiments

In all experiments, for a given temperature, saturated transport rates for NH_4^+ (ρ_T) always exceeded those for NO_3^- (Fig. 4-1). Second or third order polynomials best described the entire temperature-transport data (higher terms did not significantly improve the fit; F-test) for each experiment (Fig. 4-1, Table 4-1). T_{opt} was calculated as the temperature where $\partial\rho_T/\partial T = 0$. The value of ρ_T at T_{opt} ($\rho_{T(opt)}$) was subsequently estimated by substituting into the polynomial T_{opt} and solving for ρ_T. For maximum NO_3^- and NH_4^+ transport, T_{opt} averaged 19 ± 3 and 21 ± 2^oC (Table 4-1), with the difference between means not significant (Student's t-test; df=6). In contrast, T_{amb} averaged 11 ± 2^oC. Thus, $T_{opt} > T_{amb}$ for maximum NO_3^- and NH_4^+ transport by 9 ± 3 and 10 ± 2^oC. Differences between the mean T_{amb} and the mean T_{opt} for maximum transport of both NO_3^- and

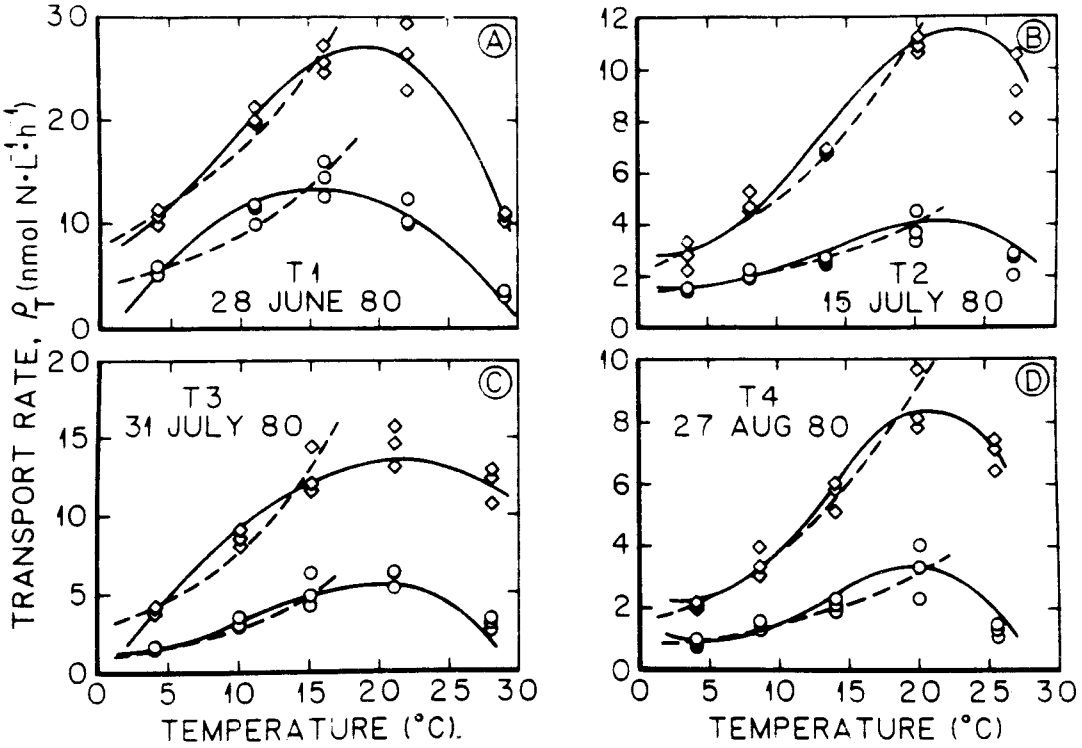

Fig. 4-1. Effect of water temperature on nitrogen-saturated rates of transport for NO_3^- (○) and NH_4^+ (◇), Toolik Lake phytoplankton. Broken curves are least squares fits of exponential functions to data over the range of increasing transport with temperature. Solid curves are least squares fits of polynomials to entire data.

Table 4-1. Regression analyses performed on data from Toolik Lake experiments examining the temperature dependence of nitrogen-saturated DIN transport, ρ_T (nmol $N \cdot L^{-1} \cdot h^{-1}$). Also, measured values of T_{amb}, DIN transport rates at T_{amb} ($\rho_{T(amb)}$) as well as calculated values of Q_{10} and T_{opt}, DIN transport at T_{opt} ($\rho_{T(opt)}$) and transport efficiencies ($\rho_{T(amb)}/\rho_{T(opt)}$).

Experiment	Date	Regression analyses: Equation	r^2	Temperature coefficient (Q_{10})[a]	Optimum temperature T_{opt}(°C)[b]	Ambient temperature T_{amb}(°C)[c]	Transport rates: $\rho_{T(opt)}$[d]	$\rho_{T(amb)}$[e]	$\rho_{T(amb)}/\rho_{T(opt)}$
T1	28 Jun 1980	$\rho_T(NO_3^-)=3.98(1.087)^T$	0.94	2.3[a]					
		$\rho_T(NO_3^-)=-1.440+1.882T-0.060T^2$	0.93		16	11	13.3	11.1	0.83
		$\rho_T(NH_4^+)=8.23(1.077)^T$	0.96	2.1					
		$\rho_T(NH_4^+)=7.285+0.481T+0.110T^2-0.0042T^3$	0.96		19	11	27.3	20.4	0.76
T2	15 Jul 1980	$\rho_T(NO_3^-)=1.29(1.061)^T$	0.94	1.8					
		$\rho_T(NO_3^-)=1.831-0.210T+0.034T^2-0.0009T^3$	0.85		22	14	4.1	2.6	0.63
		$\rho_T(NH_4^+)=2.26(1.085)^T$	0.95	2.3					
		$\rho_T(NH_4^+)=3.440-0.399T+0.081T^2-0.0021T^3$	0.95		23	14	11.6	6.9	0.59
T3	31 Jul 1980	$\rho_T(NO_3^-)=0.92(1.120)^T$	0.95	3.1					
		$\rho_T(NO_3^-)=1.566-0.230T+0.054T^2-0.0016T^3$	0.91		20	10	5.8	3.1	0.54
		$\rho_T(NH_4^+)=2.82(1.107)^T$	0.93	2.8					
		$\rho_T(NH_4^+)=-1.241+1.345T-0.031T^2$	0.88		22	10	13.3	8.5	0.64
T4	27 Aug 1980	$\rho_T(NO_3^-)=0.68(1.081)^T$	0.91	2.2					
		$\rho_T(NO_3^-)=1.953-0.453T+0.056T^2-0.0015T^3$	0.81		20	8	3.3	1.5	0.45
		$\rho_T(NH_4^+)=1.54(1.093)^T$	0.97	2.4					
		$\rho_T(NH_4^+)=3.482-0.676T+0.096T^2-0.0025T^3$	0.95		21	8	8.5	2.3	0.27

[a] Calculated from the van't Hoff expression and corresponding least squares fit of exponential to data over the range of positive response in ρ_T with increasing temperature.

[b] Temperature to nearest 1°C of greatest ρ_T predicted by corresponding least squares fit of polynomial to entire data set.

[c] Measured water temperature to nearest 1°C in incubator allowing continuous exchange of water with lake.

[d] Maximum value of ρ_T predicted from corresponding least squares fit of polynomial to entire data set.

[e] Measured mean value of ρ_T in incubator allowing continuous exchange of water with lake.

NH_4^+ were significant (Student's t-test; df=6, both cases). Pooling the entire data, there was no significant correlation between increases in T_{opt} and T_{amb} (Spearman's rank correlation coefficient; r_s=0.27; df=6). Because $T_{opt} > T_{amb}$ by ca. 9°C, DIN transport rates at T_{amb} were temperature-controlled (compare $\rho_{T(amb)}/\rho_{T(opt)}$ = transport efficiency, Table 4-1). Transport efficiencies for NO_3^- and NH_4^+ averaged 0.61±0.16 and 0.56±0.21, with the difference between means not significant (Student's t-test; df=6).

An exponential model was fitted to temperature-transport data over the range of positive response with increasing temperature for each experiment (Fig. 4-1, Table 4-1). Temperature coefficients (Q_{10}) for maximum DIN transport were then calculated from the van't Hoff relationship (Swan 1974). Mean Q_{10}s for maximum NO_3^- and NH_4^+ transport were 2.3±0.5 and 2.4±0.3, with the difference not significant (Student's t-test; df=6).

The few response curves in the literature for the interaction of temperature and maximum DIN transport vary, depending on the range of temperatures examined. Nonetheless, published data (Cloern 1977; Kappers 1980; Ullrich et al. 1981; Rhee and Gotham 1981a) agree with mine in that ρ_T increased with temperature to at least 15°C.

Interestingly, $T_{opt} >> T_{amb}$ (Table 4-1) and was, in general, physically impossible to achieve. Seaburg et al. (1981) give similar data for the temperature - *growth* response of Antarctic algal isolates. They postulated that the key physiological advantage

of these clones was their ability to grow reasonably well (although not necessarily with maximum efficiency) at cold temperatures. Likewise, psychrophilic algae may be selected in part for their ability to transport nutrients at cold temperatures with more relative efficiency than their temperate counterparts rather than for having $T_{opt} = T_{amb}$.

The rapid decrease in DIN transport at >25°C (Fig. 4-1) was possibly due to excretory loss, destruction of permeases or impairment of metabolic capacity. Similar declines in photosynthesis at supraoptimal temperatures have been variously attributed to these causes (Ahlgren 1978; Li 1980). Alternatively, ρ_T could have become phosphorus-dependent at high temperatures. Dugdale et al. (1981) showed truncated hyperbolae for nutrient uptake at the point where control shifted to another variable.

My Q_{10}s for DIN transport (Table 4-1) are somewhat lower than those given by Tischner and Lorenzen (1981) for NO_3^- transport (3.3-5.3) in *Chlorella* sp. cultures. However, from the data of Cloern (1977), Ullrich et al. (1981) and Rhee and Gotham (1981a) I calculate Q_{10}s from 2-4, similar to my data.

Indirect evidence suggests that in spite of the unused potential for N-saturated DIN transport at T_{amb} (Table 4-1), temperature had minimal effect in regulating *in situ* activity. In Toolik, DIN levels averaged about 0.25 $\mu mol \cdot L^{-1}$ (Chapter 3). For natural algal populations under similarly low nutrient regimes, Takahashi and Saijo (1981) observed no relationship between temperature and

$\rho \cdot Chl^{-1}$ for NH_4^+ (although not shown, scatter plots indicate the same here; and for NO_3^- as well), while Eppley et al. (1979) demonstrated by multiple regression analysis little influence of temperature on C-normalized NH_4^+ transport.

B. Light Dependence Experiments

In general, studies assessing light dependence have examined the ratio of dark/light-saturated DIN transport (Conway and Whitledge (1979). More specifically, for N-replete waters, the Michaelis-Menten relationship has been fitted to the data (MacIsaac and Dugdale 1972):

$$\rho = \rho_{max} \frac{I}{K_{LT} + I} \qquad (4\text{-}1)$$

where ρ is the N-saturated rate of transport at a PAR level of I and K_{LT} (half-saturation constant for PAR in N-saturated transport) is the value of I where ρ is half of the N- *and* PAR-saturated rate of transport, ρ_{max}. Data are analyzed here both ways using the following protocol: For all experiments, ρ_D/ρ_L gives the ratio of N-saturated transport in opaque/clear bottles. If transport in clear bottles was obviously depressed, values from containers permitting 48% transmission of PAR were substituted. Finally, Equation 4-1 was directly fitted to the data by the method of least squares (Cleland 1967) to evaluate kinetic parameters (K_{LT} and ρ_{max}) only when $\rho_D/\rho_L < 0.10$ (Nelson and Conway 1979). Depressed values of ρ in clear bottles were omitted in curve fitting.

Values for ρ_D/ρ_L were more variable for NO_3^- than NH_4^+, ranging over a factor of 6 for the former and 2 for the latter (Table 4-2). Means for ρ_D/ρ_L were 0.15 ± 0.09 (NO_3^-) and 0.41 ± 0.11 (NH_4^+), with the difference significant (Student's t-test; df=16).

Response curves invariably showed that at all levels of PAR, N-saturated transport for NH_4^+ exceeded that for NO_3^- (Fig. 4-2). Moreover, depressed NO_3^- transport in clear bottles was observed in two instances (Fig. 4-3B,C), possibly indicating light inhibition. Just four experiments yielded data suitable for kinetic analysis and for NO_3^- transport only (Table 4-2, Fig. 4-3). However, a light effect on maximum NH_4^+ transport was seen in all experiments at about 5-15% of PAR at 0.25 m (cf. Fig. 4-2A,B). The mean K_{LT} for NO_3^- was 16 ± 9 $\mu E \cdot m^{-2} \cdot s^{-1}$, which was about 13% of PAR at 0.25 m (Table 4-2).

Like my data, published values of ρ_D/ρ_L or V_D/V_L (mathematically equivalent) for both NO_3^- and NH_4^+ are variable, with the range given in a particular study often in excess of a factor of 3, especially for NO_3^- (Procházková et al. 1970; McCarthy et al. 1982, and others). In general, ρ_D/ρ_L averages 2-5 times greater for NH_4^+ than NO_3^-, indicating a greater light dependence of NO_3^- transport. This is in agreement with the proposed (Falkowski and Stone 1975) direct link between photosynthesis and NO_3^- utilization via the requirement for ATP from cyclic photophosphorylation to actively transport NO_3^- across the plasmalemma.

The extreme variability in ρ_D/ρ_L for NO_3^- (Table 4-2) may be

Table 4-2. PAR, chlorophyll *a*, maximum transport rates at light saturation (ρ_L) and in the dark (ρ_D), ratios of dark to light-saturated maximum transport rates (ρ_D/ρ_L) and calculated values of kinetic parameters for experiments examining the light dependence of maximum DIN transport in Toolik Lake phytoplankton.

Experiment	Date	PAR at 0.25 m ($\mu E \cdot m^{-1} \cdot s^{-1}$)	Chl *a* ($\mu g \cdot L^{-1}$)	ρ (nmol $N \cdot L^{-1} \cdot d^{-1}$)						Kinetic parameters (NO_3^-)		
				NO_3^--N			NH_4^+-N			ρ_{max}	K_{LT}	
				ρ_D	ρ_L	ρ_D/ρ_L	ρ_D	ρ_L	ρ_D/ρ_L	(nmol $\cdot L^{-1} \cdot d^{-1}$)[a]	($\mu E \cdot m^{-2} \cdot s^{-1}$)[a]	(% PAR at 0.25 m)[a,b]
LT1	13 Jul 1980	111	1.7	4	70	0.06	53	184	0.29	89	29	26
LT2	2 Aug 1980	261	1.2	14	79	0.18	70	155	0.45			
LT3	23 Aug 1980	189	1.5	3	44	0.07	46	112	0.41	55	16	8
LT4	7 Jun 1981	152	4.0	3	62	0.05	45	144	0.32	71	7	5
LT5	12 Jun 1981	282	1.2	6	27	0.22	61	121	0.50			
LT6	13 Jul 1981	124	2.1	37	119	0.31	113	217	0.52			
LT7	27 Jul 1981	232	1.2	28	118	0.24	113	197	0.57			
LT8	10 Aug 1981	87	1.0	14	88	0.16	66	183	0.36			
LT9	15 Aug 1981	91	1.2	9	95	0.09	53	196	0.27	102	12	13

[a]Values of maximum light- and nitrate-saturated NO_3^- transport rates (ρ_{max}), half-saturation constants for PAR in maximum NO_3^- transport (K_{LT}) derived from least squares fits of Michaelis-Menten relationship to data according to Cleland (1967).

[b]Values calculated as K_{LT} ($\mu E \cdot m^{-2} \cdot s^{-1}$)/$I_{0.25m}$ ($\mu E \cdot m^{-2} \cdot s^{-1}$).

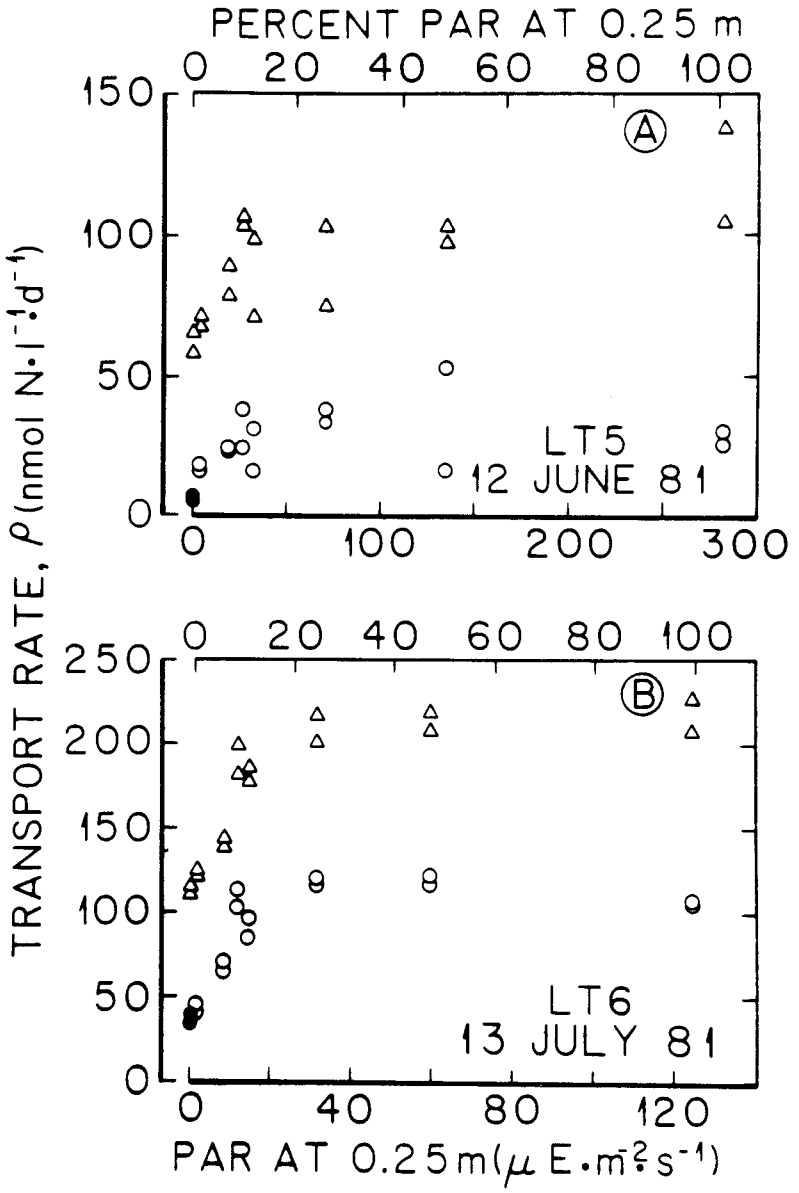

Fig. 4-2. Representative plots showing relationship between maximum NO_3^- (○) or NH_4^+ (△) transport rates and photosynthetically active radiation (PAR), Toolik Lake phytoplankton. Solid symbols are for dark transport.

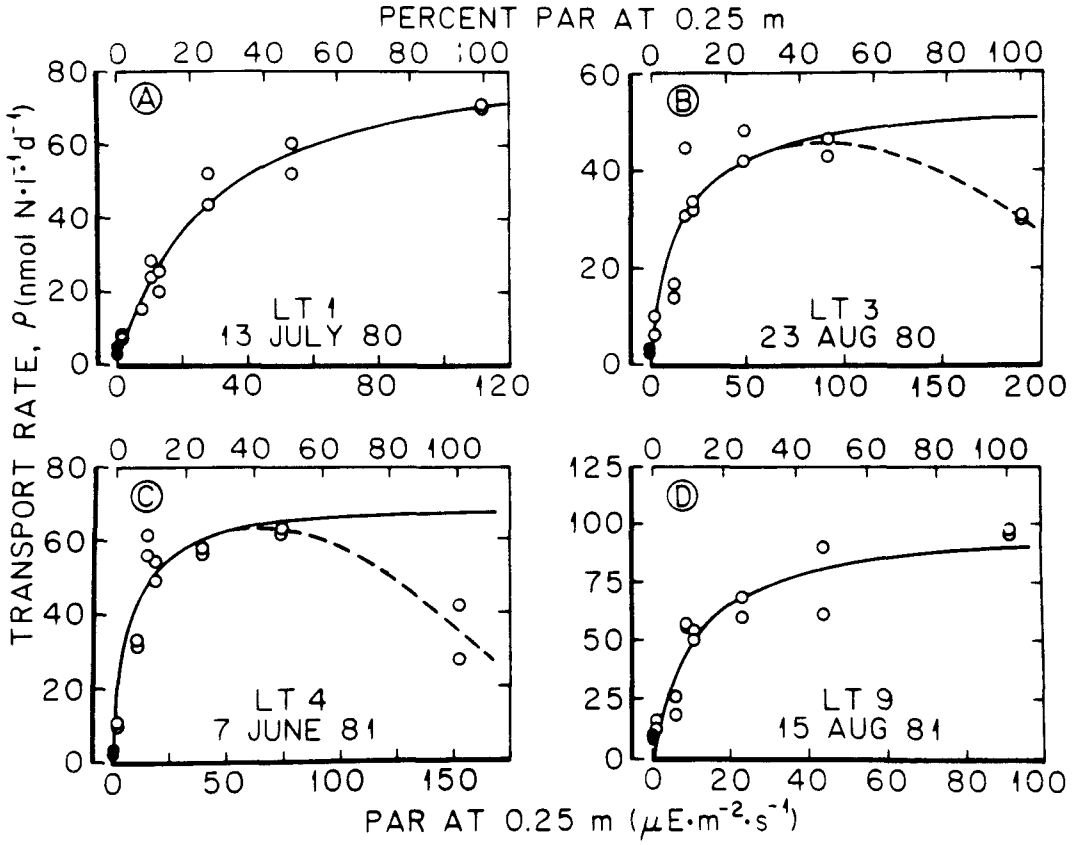

Fig. 4-3. Plots of maximum NO_3^- transport rates for Toolik Lake phytoplankton as a function of photosynthetically active radiation (PAR). Solid curves are direct, least squares fits of Michaelis-Menten relationship to data according to Equation 3-1. Broken curves in (B) and (C) are fit to data by eye. Solid symbols represent dark transport (ignored in curve fitting).

due to temporal differences in the degree of N deficiency in Toolik phytoplankton. Harrison (1976) reported enhanced dark NO_3^- transport in N-starved cultures of *Gonyaulax* sp., while Malone et al. (1975) found that NO_3^- transport in *Chaetoceros* sp. was independent of the light-dark cycle in N-limited cells but followed a diel pattern under nonlimiting conditions. Persistently low ambient DIN in experimentally manipulated Toolik waters preclude meaningful comparison with ρ_D/ρ_L for NO_3^-.

My absolute data for K_{LT} ($\mu E \cdot m^{-2} \cdot s^{-1}$) are not directly comparable to literature values which are given as $ly \cdot d^{-1}$. To facilitate comparisons, relative rates were calculated by converting PAR at 0.25 m, $I_{0.25m}$ (e.g. Table 4-2, Fig. 4-3), to percent surface PAR (I_o) using the relationship $I_o = 1.19(I_{0.25m})$ and a mean extinction coefficient of 0.7. This gave values for $K_{LT}(NO_3^-)$ ranging from 6-31% of surface PAR which corroborate well the 3-32 reported by Nelson and Conway (1979), whose guidelines were followed in selecting data to be fitted with Equation 4-1.

As was the case for temperature, PAR probably played a secondary role in regulating DIN transport in Toolik. MacIsaac and Dugdale (1972) suggested that the crossover between light- and concentration-dependent NO_3^- uptake occurs at the depth where the *in situ* rate of uptake calculated from a known K_t (half-saturation constant for NO_3^- uptake) and V_m (maximum rate of NO_3^- uptake) in Equation 2-1 is greater than the measured-enhanced rate. This point was never reached during the ice-free period due to low am-

bient NO_3^- (Fig. 4-4). The calculated crossover point to regulation solely by PAR at 8 m is about 2.8 $\mu mol \cdot L^{-1}$ NO_3^-, a concentration reached only in the early spring beneath ice cover (Chapter 3).

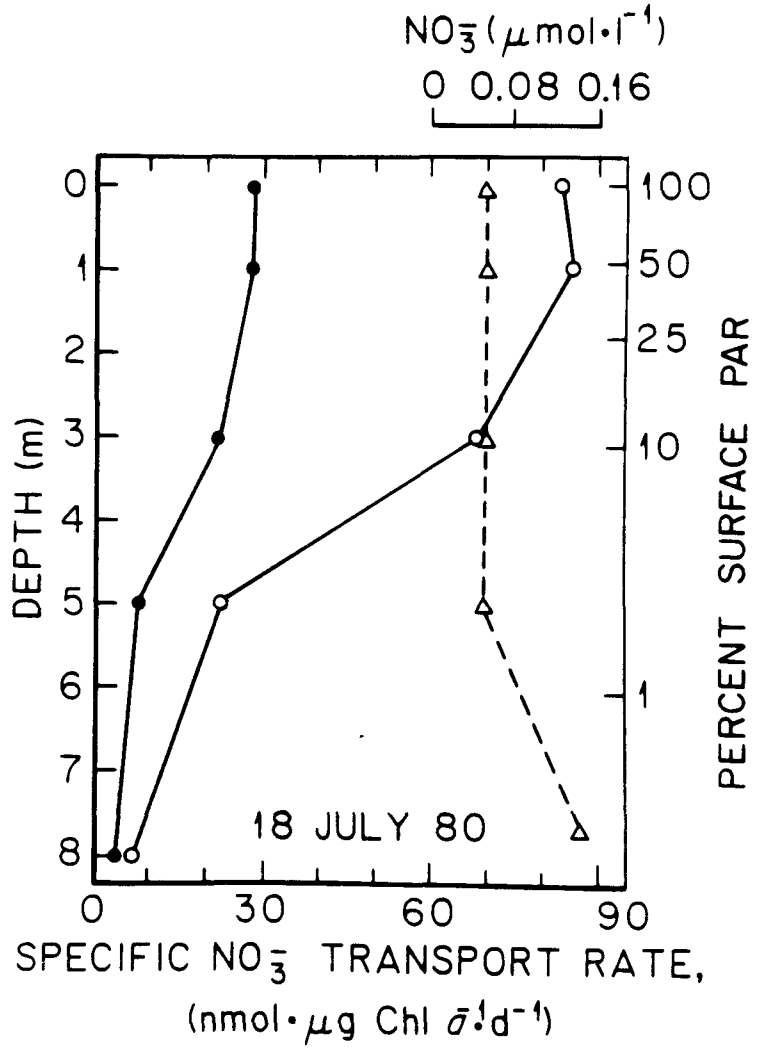

Fig. 4-4. Depth profiles of chlorophyll-specific NO_3^- transport ($\rho \cdot Chl^{-1}$) and ambient NO_3^-, Toolik Lake. ○, measured-enhanced $\rho \cdot Chl^{-1}$ following addition of 3.07 µmol·L^{-1} $^{15}NO_3^-$; ●, *in situ* rates calculated from Michaelis-Menten relationship (K_t=0.12 µmol·L^{-1}, $[\rho \cdot Chl^{-1}]_m$ calculated from measured-enhanced $\rho \cdot Chl^{-1}$); △, ambient NO_3^-. Details of calculations given in MacIsaac and Dugdale (1972).

CHAPTER 5. CHEMICAL INFLUENCES ON PHYTOPLANKTON TRANSPORT OF DIC AND DIN

Introduction

Beyond the macronutrients N and P, phytoplankton nutrient requirements include vitamins (Bonin et al. 1981) and trace metals (Huntsman and Sunda 1980). Although not directly active in metabolic processes, organic complexing agents (e.g. humic and fulvic acids) are often considered essential algal nutrients due to their capacity to bind metal ions, simultaneously reducing activity but maintaining them in solution (Reynolds 1984). Elucidation of chemical influences on productivity is central to studies of algal ecology and all of these factors have at some time been implicated as regulators of primary biosynthesis in aquatic environments (reviewed by Maestrini et al. 1984).

The most popular method of assessing nutrient deficiency is the differential enrichment bioassay where stimulation of some response index indicates that the nutrient in question is in short supply. Enrichment bioassays are by no means new, having been introduced by Allen and Nelson in 1910. However, early experiments relied on cumbersome "state" measurements (dry weight, cell counts or volume) as the response index. Modern field bioassays sometimes include these as well but almost universally have embraced the simple and sensitive "rate" measurement, ^{14}C transport, pioneered by Ryther and Guillard (1959) as the index of response.

Methods for nutrient bioassays are unstandardized, rendering

difficult comparison of results among investigations. The variety of experimental designs reflects ongoing identification of those which may confound results or lead to erroneous data interpretation, not only in bioassays but in measurements of *in situ* productivity.

Any scheme, therefore, represents a compromise weighing the designer-perceived merits and disadvantages of each protocol for the system of interest. For example, choice of response index is crucial when making state measurements over several days as a treatment may give a positive response in one, yet elicit no change in a second (Paerl 1982). Alternatively, depending on the level of enrichment, a variable response may be shown by both state (Stoermer et al. 1978) and rate (Lean et al. 1982) indices for a single treatment. Length of incubation is important as it must exceed the initial period of lag or suppression in ^{14}C transport following addition of a deficient nutrient (Lean and Pick 1981). On the other hand, it must not be excessive to avoid "bottle effects" which impair photosynthesis in lengthy containment of small samples (Venrick et al. 1977).

These numerous problems have recently spawned the development of short-term physiological assays of phytoplankton nutritional status. In particular, techniques devised to detect N deficiency subsequent to my study include measurement of rates of DIN assimilation into protein (Glibert and McCarthy 1984) as well as determination of ratios for intracellular amino acid/protein

(Dortch et al. 1985) and DIN transport at saturating/ambient levels (Glibert and McCarthy 1984).

Specific goals of this component were to (a) identify with ^{14}C bioassays important chemical factors regulating photosynthesis, the common measure of algal productivity, (b) corroborate results with those from ^{15}N bioassays which may give a better indication of chemical controls over primary biosynthesis as N storage and luxury uptake are minimal and (c) interpret these seasonal data in the context of the limnological paradigm (Hutchinson 1967) that nutrient deficiency develops during summer in dimictic lakes, but is absent during vernal and autumnal circulation when hypolimnetic nutrients are made available to euphotic waters.

My use of ^{15}N bioassays is fairly novel as this technique has been employed only once previously (Axler and Goldman 1981) and to a more limited extent. A surprising data base exists for bottle and whole pond bioassays in high latitudes (see Results and Discussion), but mine are the first seasonal data for a deep arctic lake.

Methods

On twelve dates during 1980 and 1981 (coded consecutively P1-P12), mid-epilimnetic water was collected initially into ten clear 20-L polyethylene carboys. Each received one of the following additives: (a) no addition (control), (b) 3 $\mu mol \cdot L^{-1}$ KNO_3, (c) 3 $\mu mol \cdot L^{-1}$ NH_4Cl, (d) 0.5 $\mu mol \cdot L^{-1}$ H_2PO_4, (e) treatments b-d in combination (designated "N+P"), (f) 0.03 $\mu mol \cdot L^{-1}$ Na_2MoO_4,

(g) a trace metal-disodium ethylenediaminetetraacetate mixture (Na_2EDTA) consisting of 0.03 $\mu mol \cdot L^{-1}$ $MnCl_2$ and $ZnCl_4$, 0.015 $\mu mol \cdot L^{-1}$ $CoCl_2$ and $CuSO_4$, 0.12 $\mu mol \cdot L^{-1}$ $FeCl_3$ and 0.3 $\mu mol \cdot L^{-1}$ Na_2EDTA, (h) 0.3 $\mu mol \cdot L^{-1}$ Na_2EDTA, (i) a vitamin mixture consisting of 1 $nmol \cdot L^{-1}$ each of biotin, cyanocobalamin and thiamin or (j) a salt mixture of 2 $\mu mol \cdot L^{-1}$ NaCl and 1 $\mu mol \cdot L^{-1}$ K_2SO_4.

All additives were small enough to avoid arresting or retarding phytoplankton activity. However, they were sufficient to sizeably increase (40->100%) ambient levels based on known concentrations for Toolik or published values for arctic or other oligotrophic fresh waters. Treatment (h) represented addition of a commonly used synthetic chelate (Maestrini et al. 1984) while (g) incorporated both the chelate and trace metals most important to algae (Ryther and Roth 1971), less Mo. Molybdenum was isolated in treatment (f) because it has been demonstrated to regulate both DIC and NO_3^- transport in an oligotrophic lake (Axler et al. 1980) and (i) included all the vitamin requirements of auxotrophic algae (Provasoli and Carlucci 1974). The salt mixture (j) was used to isolate the effects of the other test nutrients from a response resulting from a shift in the monovalent/divalent ion ratio accompanying addition of a nutrient salt. This change in itself can alter rates of photosynthesis (Fogg 1965).

After mixing, carboys were screened to exclude 50% of the incident irradiance and placed in the lake surface for 6 h. Water was then dispensed into appropriate containers to measure ^{14}C (3 or

4 light plus a single dark bottle, each treatment) or ^{15}N (3 bottles, each DIN species and treatment) transport, injected with isotope and suspended at 1 m for 24 h.

This experimental design circumvented the acknowledged problems with bioassays but complicated data analysis. Coefficients of variation associated with the replicate ^{14}C transport determinations in samples from the control, nitrate- and ammonium-amended carboys for all experiments averaged 9, 9 and 10%. Within-carboy CVs for ^{14}C, $^{15}NO_3^-$ and $^{15}NH_4^+$ transport were similar for all other treatments. In four closely allied experiments in 1979, among-container CVs (single determination of ^{14}C transport from triplicate containers, each treatment) for control, nitrate- and ammonium-treated samples averaged no worse than within-container CVs here, 6, 6 and 6%. Consequently, differences in mean rates of isotope incorporation for replicate samples drawn from carboys were assumed to be treatment-related. Thus, untransformed data (variances homogeneous in all cases; F_{max} test) for each experiment were analyzed by single-factor ANOVA and Student-Newman-Keuls test (SNK) for the effect of nutrient addition on ^{14}C and ^{15}N transport. Only values of $P<0.01$ were considered significant for statistical analyses in this study component.

Total dissolved phosphorus determinations were completed by J.C. Cornwell according to standard techniques (Cornwell 1983).

Results and Discussion

Low ambient nutrient and Chl a levels for bioassay experiments (Table 5-1) are in concordance with data given in Chapter 3 and further emphasize the oligotrophy of Toolik Lake.

In all ^{14}C bioassays one or more treatments differed significantly from the others (Fig. 5-1). The data showed a clear trend toward stimulation of $\rho(C)$ in N+P- or N-amended samples relative to the majority of treatments. In four experiments (P2, P8, P10, P11), N+P addition alone gave the best response while N+P and some form of DIN enhanced transport to an equal and significant extent in four additional instances (P5, P7, P9, P12). In the single case where N+P was not administered, P1, addition of either form of DIN accelerated $\rho(C)$. The general stimulatory effect of N+P and DIN on $\rho(C)$ was obviously not limited to the period of thermal stratification as distinctly orthograde temperature profiles characterized P5 and P12 (cf. Figs. 5-1, 5-2).

As for ^{14}C bioassays, all $^{15}NO_3^-$ bioassays showed one or more treatments that differed significantly from the others (Fig. 5-3). In all experiments, exposure to NH_4^+ resulted in depressed $\rho(NO_3^-)$, while in seven instances (P1-P4, P6-P8) PO_4^{3-} addition enhanced transport.

In $^{15}NH_4^+$ bioassay P10 no treatment differed significantly, but for all other cases some treatment was different from the majority (Fig. 5-4). Like their $^{15}NO_3^-$ counterparts, $^{15}NH_4^+$ bioassays showed increased transport in PO_4^{3-}-enriched samples on seven occasions

Table 5-1. Mid-epilimnetic concentrations of nutrients as $\mu mol \cdot L^{-1}$ and chlorophyll a (±SD) as $\mu g \cdot L^{-1}$ in Toolik Lake during bioassay experiments.

Experiment	Date	NO_3^--N	NH_4^+-N	Total dissolved-P	Chlorophyll a
P1	9 Jul 80	0.03	0.15	0.22	2.3 (0.1)
P2	26 Jul	0.03	0.17	0.10	1.0 (0.1)
P3	24 Aug	0.06	0.13	0.10	1.5 (0)
P4	7 Jun 81	0.07	0.05	0.09	5.9 (0.1)
P5	13 Jun	0.04	0.25	0.08	1.4 (0)
P6	11 Jul	0.11	0.09	0.10	2.6 (0.1)
P7	25 Jul	0.06	0.25	0.32	1.2 (0)
P8	1 Aug	0.08	0.23	0.07	1.1 (0.1)
P9	8 Aug	0.03	0.15	0.07	1.0 (0)
P10	13 Aug	0.04	0.15	0.10	1.0 (0.1)
P11	18 Aug	0.03	0.28	0.09	1.3 (0.1)
P12	29 Aug	0.05	0.12	0.07	1.5 (0.1)

EXPT	DATE	TREATMENT									
P1	9 JUL 80	VIT	TMEDTA	CONT	MO	SALT	EDTA	PO4	NH4	NO3	
		1282	1527	1533	1545	1565	1711	1791	2301	2441	
P2	26 JUL 80	SALT	MO	CONT	VIT	NO3	PO4	TMEDTA	EDTA	NH4	N+P
		407	472	475	485	542	572	591	595	682	911
P3	24 AUG 80	EDTA	SALT	TMEDTA	PO4	MO	CONT	NH4	NO3	N+P	VIT
		322	337	362	365	368	378	417	417	418	433
P4	7 JUN 81	TMEDTA	VIT	EDTA	CONT	SALT	PO4	N+P	NH4	MO	NO3
		3938	4763	4907	5065	5464	5642	6812	6826	7159	7312
P5	13 JUN 81	EDTA	VIT	CONT	PO4	SALT	TMEDTA	MO	NH4	NO3	N+P
		1440	1665	1760	1852	1872	1900	1977	2343	2636	2717
P6	11 JUL 81	VIT	TMEDTA	EDTA	CONT	MO	NO3	NH4	PO4	SALT	N+P
		1285	1375	1527	1588	1629	1826	1992	2023	2309	2333
P7	25 JUL 81	PO4	SALT	CONT	VIT	TMEDTA	MO	EDTA	NH4	NO3	N+P
		1408	1822	1831	1835	1890	1967	1991	2543	2734	3038
P8	1 AUG 81	PO4	SALT	CONT	MO	VIT	EDTA	NO3	TMEDTA	NH4	N+P
		667	727	802	857	926	1028	1080	1084	1199	1634
P9	8 AUG 81	VIT	EDTA	CONT	SALT	PO4	MO	TMEDTA	NO3	NH4	N+P
		1397	1608	1729	1783	1849	1943	1952	2567	3009	3178
P10	13 AUG 81	VIT	CONT	PO4	MO	SALT	EDTA	TMEDTA	NO3	NH4	N+P
		639	687	726	783	822	906	981	1230	1335	1831
P11	18 AUG 81	VIT	SALT	CONT	PO4	MO	EDTA	NO3	TMEDTA	NH4	N+P
		1355	1370	1410	1442	1444	1466	1667	1779	1968	2613
P12	29 AUG 81	VIT	PO4	MO	EDTA	SALT	TMEDTA	NO3	CONT	NH4	N+P
		994	1039	1163	1165	1169	1215	1353	1368	1621	1630

Fig. 5-1. Results of Student-Newman-Keuls test ($P<0.01$) for multiple comparisons among treatment means in ^{14}C bioassays, Toolik Lake phytoplankton, when a multi-sample hypothesis of equal means was rejected by single-factor ANOVA ($P<0.01$). For each experiment, treatment means are arranged in order of ascending dissolved inorganic carbon (DIC) transport ($nmol \cdot L^{-1} \cdot d^{-1}$). Treatments not underscored by same line show significantly different DIC transport rates; those underscored by same line have rates that are not significantly different. Treatment codes: CONT = control (no addition); EDTA = Na_2EDTA alone; TMEDTA = trace metals + Na_2EDTA; MO = Na_2MoO_4; SALT = NaCl + K_2SO_4; PO4 = PO_4^{3-}; NO3 = NO_3^-; NH4 = NH_4^+; N+P = NO_3^- + NH_4^+ + PO_4^{3-}; VIT = vitamins. Details in text.

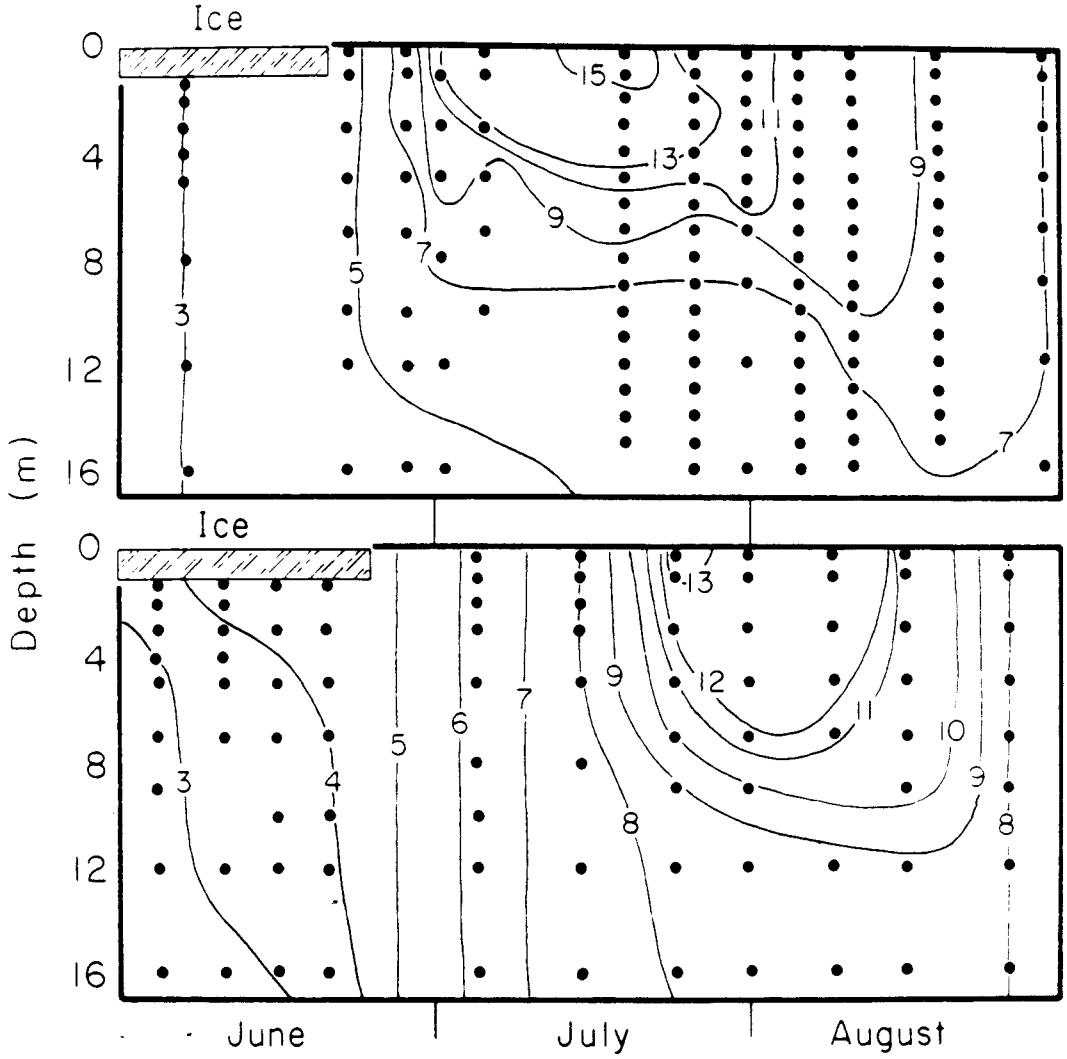

Fig. 5-2. Isotherms (°C) for Toolik Lake in 1980 (top) and 1981 (bottom).

EXPT	DATE	TREATMENT							
P1	9 JUL 80	NH4	CONT	SALT	MO	VIT	TMEDTA	EDTA	PO4
		30	173	183	183	185	187	191	244
P2	26 JUL 80	NH4	VIT	CONT	TMEDTA	SALT	EDTA	MO	PO4
		12	78	78	80	83	84	88	108
P3	24 AUG 80	NH4	EDTA	CONT	SALT	TMEDTA	MO	VIT	PO4
		7	47	53	57	58	58	60	77
P4	7 JUN 81	NH4	TMEDTA	CONT	SALT	VIT	EDTA	MO	PO4
		28	57	75	76	77	79	79	108
P5	13 JUN 81	NH4	EDTA	PO4	TMEDTA	VIT	SALT	CONT	MO
		6	9	29	41	43	43	46	49
P6	11 JUL 81	NH4	MO	VIT	TMEDTA	EDTA	CONT	SALT	PO4
		27	59	60	63	67	71	78	107
P7	25 JUL 81	NH4	VIT	CONT	EDTA	SALT	TMEDTA	MO	PO4
		11	68	71	71	76	77	83	108
P8	1 AUG 81	NH4	SALT	CONT	MO	TMEDTA	EDTA	VIT	PO4
		19	68	68	74	76	80	83	99
P9	8 AUG 81	NH4	VIT	TMEDTA	EDTA	CONT	SALT	MO	PO4
		9	59	68	72	74	81	81	91
P10	13 AUG 81	NH4	VIT	EDTA	CONT	TMEDTA	SALT	MO	PO4
		11	40	46	48	48	49	50	56
P11	18 AUG 81	NH4	SALT	EDTA	CONT	TMEDTA	MO	VIT	PO4
		14	66	71	73	76	76	81	90
P12	29 AUG 81	NH4	CONT	VIT	EDTA	SALT	TMEDTA	MO	PO4
		13	51	51	52	55	57	59	67

Fig. 5-3. Results of $^{15}NO_3^-$ bioassays, Toolik Lake phytoplankton. As Fig. 5-1. but with data arranged in order of increasing NO_3^- transport ($nmol \cdot L^{-1} \cdot d^{-1}$).

(P1, P3, P4, P6-P9). However, unlike $^{15}NO_3^-$ experiments, exposure to the alternate form of DIN did not universally lead to depressed transport, but rather in three instances only (P1, P7, P9).

For both DI^{15}N bioassay types, the stimulatory influence of PO_4^{3-} was probably independent of the temperature structure of the lake. Accelerated transport for both $^{15}NO_3^-$ and $^{15}NH_4^+$ was observed in P3, P4 and P6, when there was no thermal resistance to mixing (cf. Fig. 5-2, Fig. 5-3, Fig. 5-4).

Widely disparate results have been obtained for ^{14}C bioassays in polar regions. For example, N (Kalff 1971; Hawes 1983), P (Kalff 1971; Stanley and Daley 1976; Alexander et al. 1980; Hawes 1983), trace metals (Kalff 1971; O'Brien 1975) and CO_2 (Hawes 1983) have been implicated as important regulatory agents seasonally for shallow tundra ponds and waters of the Noatak drainage in Alaska and for maritime Antarctic lakes.

Except for Hawes (1983), none of these investigators included as a treatment simultaneous addition of N and P. My data compare favorably with those from arctic waters where this was used, but the response index was a long-term (several days) measurement of state. Tube experiments in Char Lake (Schindler et al. 1974b), batch bioassays and fertilization of entire ponds on the Colville River, Alaska flood plain (McCoy 1983) and continuous flow periphyton bioassays in the Kuparuk River, Alaska (Peterson et al. 1983) all yielded the greatest biomass increase with N+P enrichment.

The limited published data exploring the interaction between algal transport systems for DIN and PO_4^{3-} show conflicting results and are not directly comparable to mine due to differences in incubation times. Therefore, I can only speculate as to the cause for increased DIN transport in phosphate-amended samples (Figs. 5-3, 5-4). Healey (1979) noted that cellular ATP increased in P-deficient algal cultures within hours of PO_4^{3-} addition. He argued that this response was logical because active transport and incorporation into metabolites or storage products is an energy-requiring process. If Toolik phytoplankton were both N- and P-deficient, enrichment with PO_4^{3-} and a 6 h acclimation may have provided, respectively, the substrate and time necessary for *de novo* ATP synthesis. Ultimately, this would maximize exploitation of added $DI^{15}N$.

The depressed $\rho(NO_3^-)$ universally seen here in response to NH_4^+ addition (Fig. 5-3) is consistent with the voluminous literature demonstrating both that NH_4^+ is the preferred form of DIN and that its presence at ca. >1 $\mu mol \cdot L^{-1}$ suppresses NO_3^- transport (reviewed by McCarthy 1980).

Reduced $\rho(NH_4^+)$ on three occasions following exposure to NO_3^- (Fig. 5-4) is not as easily explained. The $^{14}NO_3^-$ spike may have saturated algal DIN demands during the 6 h acclimation, yielding a diminished time-integrated response in $\rho(NH_4^+)$. Alternatively, the indiginous population may have been particularly N-deficient, with simultaneous transport of $^{14}NO_3^-$ and $^{15}NH_4^+$ occurring after addition

of the latter. Such partitioning would lead to reduced tracer incorporation if both transport mechanisms were competing for the same finite energy resource. Conway (1977) showed that inhibition of NO_3^- uptake by NH_4^+ in continuous cultures of marine algae decreased with increasing NH_4^+ deficiency.

The indifference of the stimulatory effects of N+P or N (^{14}C bioassays) and PO_4^{3-} (^{15}N bioassays) to the thermal structure of the lake is not surprising. Internal nutrient loading rates are the lowest recorded for freshwaters (Chapter 3 and Cornwell 1983), precluding formation of a nutricline and hypolimnetic storage during the brief summer stratification.

Results of bioassays are by no means incontestable. Thus, I cautiously summarize these data as simply suggesting chronic N and P deficiency in Toolik phytoplankton.

CHAPTER 6. DIEL PERIODICITY OF DIC AND DIN TRANSPORT BY PHYTOPLANKTON

Introduction

The ubiquitous diel periodicity in both photosynthetic capacity and light-limited photosynthesis (reviewed by Sournia 1974) has long fascinated phycologists. However, this phenomenon has been the scourge of field biologists as it renders difficult assessment of *in situ* day-rates (i.e. over 24 h) of productivity. Albeit impractical on a large scale, the best estimate involves summation of results from consecutive short-term incubations over an entire day (Tilzer et al. 1977). In general, reported rates derive from experiments lasting 24 h or a fraction of a day. The former may give underestimates due to bottle effects (Venrick et al. 1977). With appropriate qualifying statements, the latter have been extrapolated to 24 h from theoretical considerations (Vollenweider 1965) or by assuming proportionality between irradiance and productivity (Wetzel 1964).

Although less intensely investigated, diel variations for *in situ* DIN uptake (transport) have also been reported (Goering et al. 1964). Experimental protocol for determining daily transport of DIN is poorly defined, perhaps because of problems inherent with stable tracer methodology and physiological differences between DIC and DIN transport in autotrophs.

Fundamental assumptions in making *in situ* rate measurements with tracers include: (a) nondisruption of the steady state by

isotope addition (Harrison 1983) and (b) constancy of isotope enrichment of the aqueous phase in the form added over the period of study (Garside 1984). Even in low alkalinity waters, amendment with small quantities of carrier-free radiocarbon affords sensitive determination of photosynthetic activity while adhering to these principles. In contrast, for N-poor waters, addition of even the generally accepted minimum of ^{15}N tracer (0.05 $\mu mol \cdot L^{-1}$; Glibert et al. 1982) necessary for adequate incorporation into the particulate fraction and concurrent release of cellular $^{14}NH_4^+$ during incubation (Goldman and Glibert 1983) result in nearly unavoidable violations of these assumptions. Moreover, at low concentrations, the less direct dependence of DIN transport on PAR (Falkowski and Stone 1975) precludes reasonable extrapolation of results from a short exposure to day-rate activity in the manner customary for DIC.

A precursor to meaningful seasonal assessment of phytoplankton DIC and DIN transport is accurate estimation of daily activity. Therefore, the primary purpose of this study component was to establish guidelines to reasonably extrapolate 24 h field measurements of DIC and maximum DIN transport to *in situ* day-rates. Secondarily, I wanted to test for a diel rhythmicity of transport for these nutrients in high latitude communities. To these ends I have utilized time-series and time-course analyses. The former involves repetitive occupation of a single lake station and the latter periodic sampling from a single homogeneous population.

Methods

Three time-series experiments (designated D1-D3) were conducted on 1 and 18 July and 5 August 1980. Each consisted of six consecutive *in situ* incubations of 6 h duration in which DIC and maximum DIN uptake (transport) were measured at 0, 1, 3, 5 and 8 m (for each depth: DIC, 3 light and 1 dark bottle; NO_3^- and NH_4^+, 2 bottles each species). The first incubation began at 0600 local time and the sixth ended at 1800 on the second day.

An additional set of bottles was suspended for 24 h beginning and ending at 0600 on the first and second days such that the period of exposure encompassed the first four 6 h incubations of the time-series. Kinetic experiments of 4 h duration (discussed more extensively in Chapter 7) were conducted in conjunction with each time-series to derive half-saturation constants for NO_3^- and NH_4^+ transport to back-calculate via Equation 2-1 to rates of activity at ambient nutrient levels. The entire suite of necessary chemical determinations (PN, DIN, pH and alkalinity) was made for each depth during each of the six incubations comprising a time-series.

Two time-course experiments (labeled IT1, IT2) were implemented on 2 and 7 July 1982 to examine the effect of duration of incubation on ^{15}N incorporation into the particulate fraction. Mid-epilimnetic water was collected at 1200 local time into sample bottles which were held at 50% incident irradiance for 6 h until the temperature was raised from that at the depth of collection

(10-12°C) to the laboratory temperature (15°C). Following addition of an uptake-saturating concentration of $^{15}NO_3^-$ or $^{15}NH_4^+$, samples were placed under a bank of fluorescent lights and withdrawn (3 bottles, each DIN species) at 2, 4 and 6 h and at 3 h increments thereafter to a maximum incubation time of 24 h. All remaining bottles were shaken hourly to resuspend the contents. Photosynthetically active radiation was held constant at 33 $\mu E \cdot m^{-2} \cdot s^{-1}$ and $< \pm 1.5$°C fluctuations in sample temperature were noted in hourly monitoring. Results were normalized to 15°C with a Q_{10} of 2.4 (Chapter 4).

Results and Discussion

Concordant with data from Chapter 3, depth profiles for DIN in time-series experiments showed little vertical structure, with NO_3^- and NH_4^+ averaging around 0.05 and 0.13 $\mu mol \cdot L^{-1}$. Biomass (PN) was homogeneously distributed at around 2 $\mu mol \cdot L^{-1}$ in D2 and D3, but had a distinct maximum at 5 m (ca. 4 $\mu mol \cdot L^{-1}$ vs. 3 elsewhere) in D1. For a particular depth, DIN and PN showed no discernible rhythmicity over 36 h in any experiment. In contrast, temporal and depth variations in PAR (Fig. 6-1) and temperature, respectively, were clearly evident. Isotherms (Fig. 5-2) indicated a thermocline from 1-8 m in D1 and D2 and from 8-12 m in D3. The selected sample depths corresponded to those of 100, 51, 13, 3 and 0.4% penetration of surface PAR.

Kinetic studies (Fig. 6-2) done in conjunction with time-

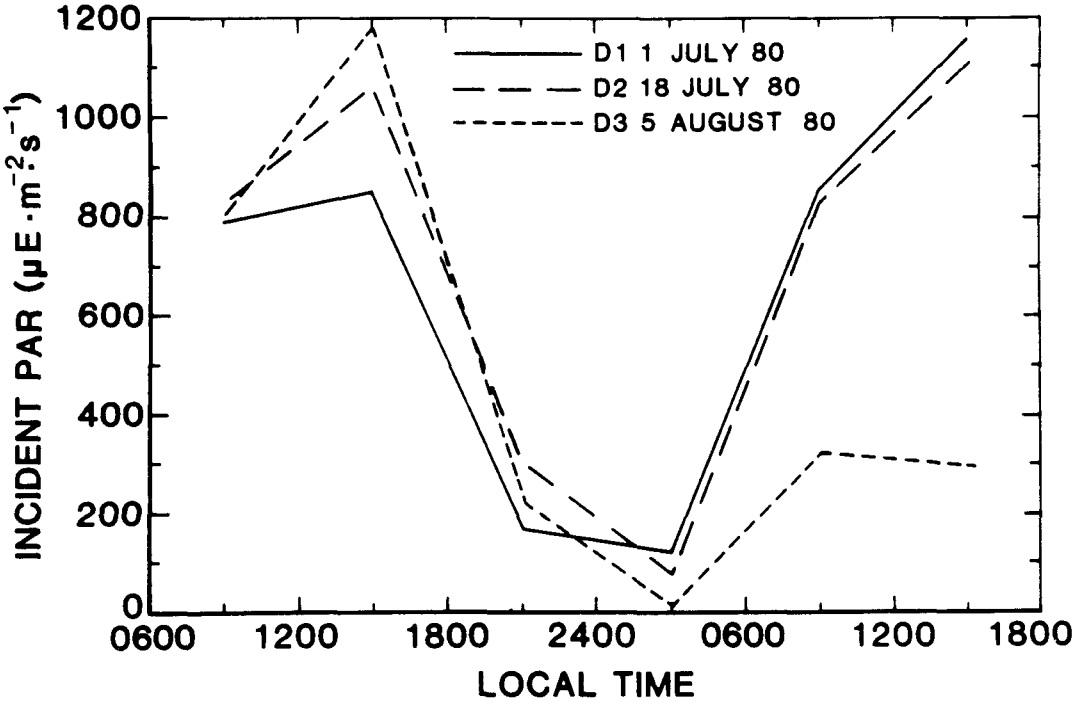

Fig. 6-1. Variations in incident photosynthetically active radiation (PAR) in time-series experiments, Toolik Lake. Average value plotted at midpoint of each 6 h incubation.

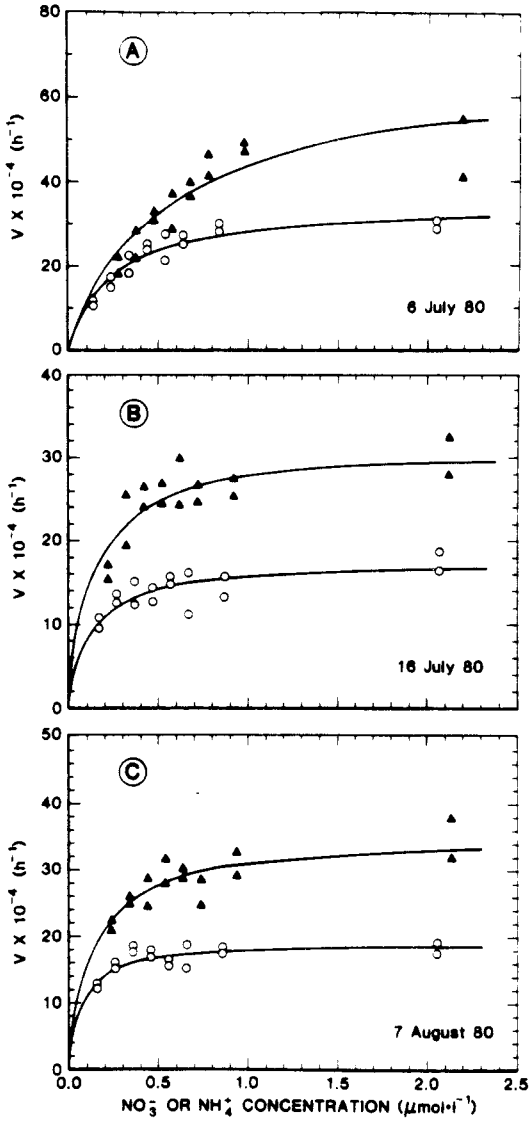

Fig. 6-2. Uptake rates (V) for NO_3^- (○) and NH_4^+ (▲) by Toolik Lake phytoplankton as a function of substrate level. Each curve is a least squares fit of Michaelis-Menten relationship to uptake - concentration data.

series analyses gave values of 0.25, 0.12 and 0.07 $\mu mol \cdot L^{-1}$ for $K_t(NO_3^-)$ and 0.49, 0.17 and 0.15 $\mu mol \cdot L^{-1}$ for $K_t(NH_4^+)$ in D1, D2 and D3, respectively.

Maximum uptake rates for DIN in time-series showed a similar pattern in all three experiments (illustrated by D1; Fig. 6-3). Variations in $V_m(NO_3^-)$ and $V_m(NH_4^+)$ from 0-5 m were virtually isochronal, but of differing magnitudes.

Log-transformations of V_m homogenized variances (F_{max} test) and data within each experiment were analyzed by two-factor ANOVA with depth and incubation period as the main effects. In three experiments where no time-depth interactions were noted (D1, NH_4^+; D2, NO_3^- and NH_4^+), V_m was significantly affected by depth and time of day. Multiple comparisons among treatment levels by SNK (Fig. 6-4) indicated that in the absence of an interaction effect, depth had no influence on $V_m(NO_3^-)$ or $V_m(NH_4^+)$ to 3 m. However, at 5 and 8 m maximum uptake rates were significantly reduced from shallower depths (Fig. 6-3B). No obvious pattern was found for $V_m(NH_4^+)$ when incubation periods were compared by SNK, but for $V_m(NO_3^-)$ a nighttime minimum was observed (Fig. 6-4). Although not tested statistically, these trends (reduced V_m at 5 and 8 m; evening decrease in $V_m(NO_3^-)$) appeared to hold for experiments with time-depth interactions (Fig. 6-3A).

A diel periodicity was obvious for $\rho(C)$ in all experiments (illustrated by D1; Fig. 6-5A). However, data analysis is not so straightforward for $\rho(NO_3^-)$ and $\rho(NH_4^+)$. Unlike directly determined

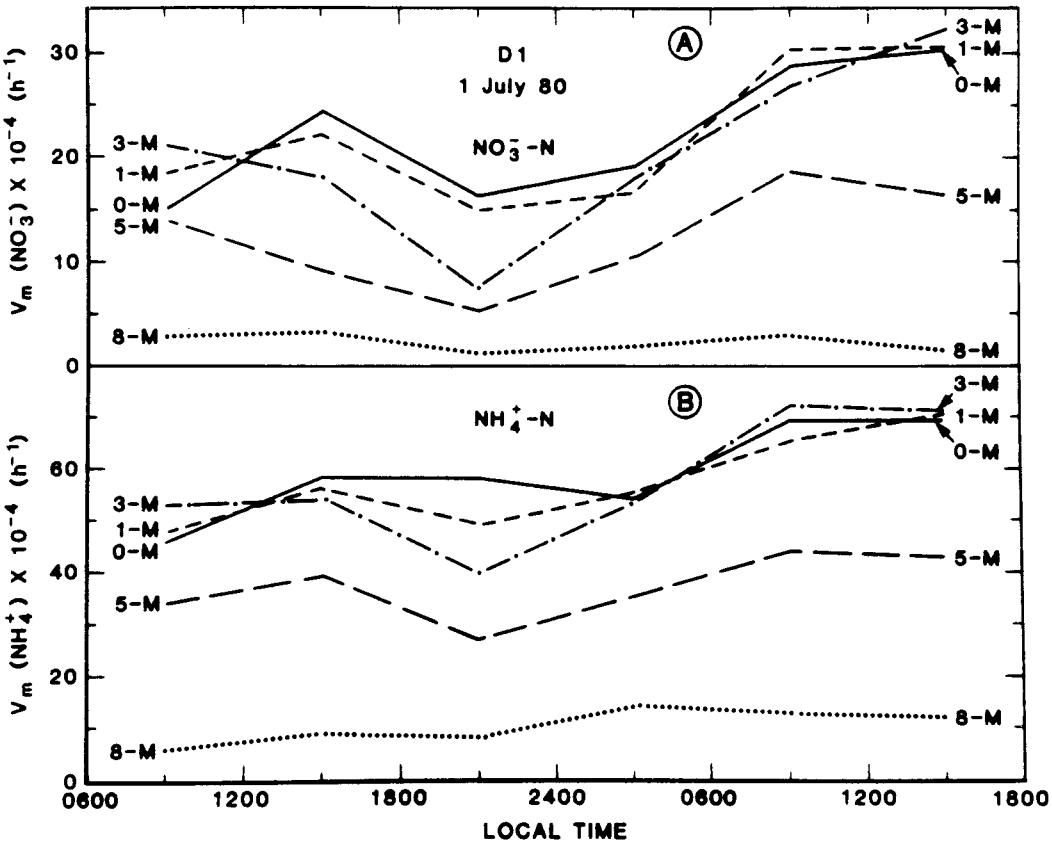

Fig. 6-3. Time and depth variations in maximum specific uptake rates (V_m) for NO_3^- and NH_4^+, Toolik Lake phytoplankton. Data from each depth plotted at midpoint of each 6 h incubation period.

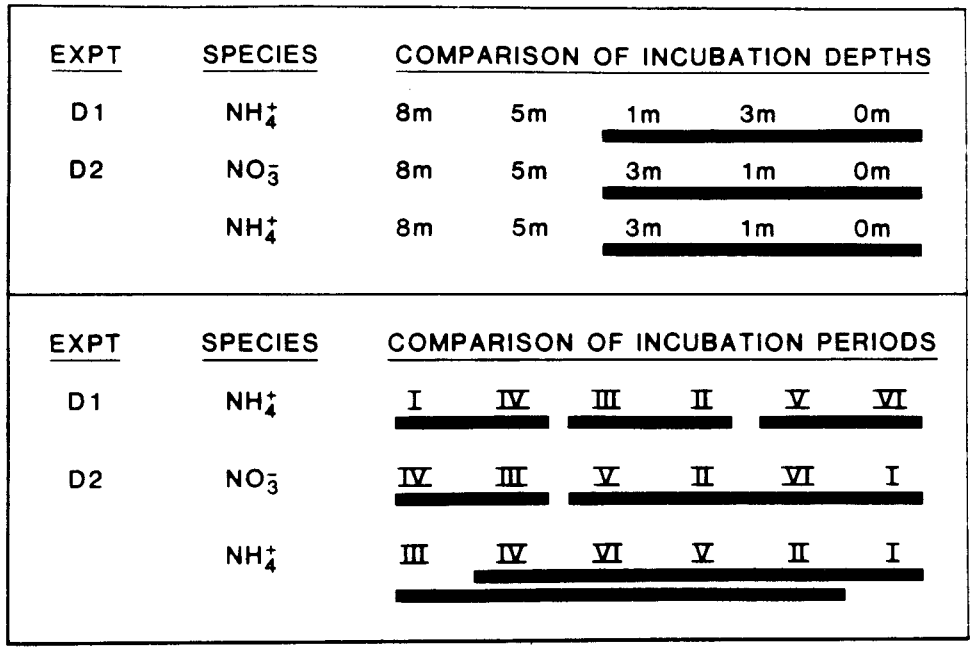

Fig. 6-4. Results of Student-Newman-Keuls test ($P<0.05$) assessing differences among main effects (depth or incubation period) on maximum NO_3^- and NH_4^+ uptake rates (V_m) in time-series experiments, Toolik Lake phytoplankton, where no significant time - depth interactions were found in two-factor ANOVA ($P<0.05$). In a given experiment, depths are arranged in order of increasing V_m. Incubation periods are numbered consecutively I (06:00-12:00, first day) through VI (12:00-18:00, second day) and are arranged in order of increasing V_m. Incubation periods or depths not underscored by same line have significantly different values of V_m for the treatment in question. Those underscored by same line have values of V_m that are not significantly different.

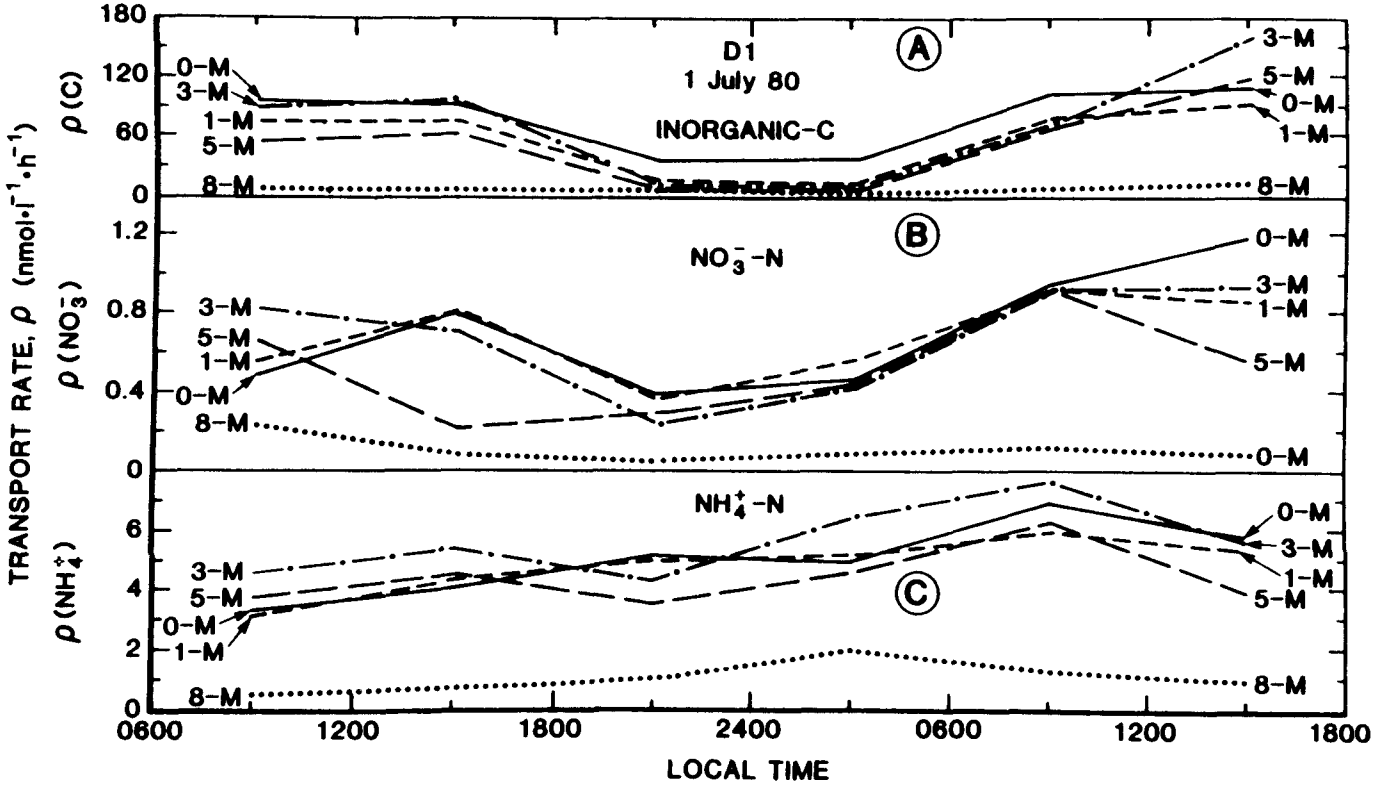

Fig. 6-5. Time - depth variations in transport rates (ρ) for inorganic carbon, NO_3^- and NH_4^+, Toolik Lake phytoplankton. Data for each depth plotted at midpoint of each 6 h incubation period.

values for V_m, back-calculation (Equation 2-1) from kinetic and ambient nutrient data to estimate *in situ* values for ρ reflected changes in biomass or nutrient concentration, whether real or due to random analytical errors. This is because ρ is the product of V times PN (Chapter 2) and changes in ρ are approximately first order with respect to variations in nutrients at typical ambient levels (Fig. 6-2). Such extrapolation suggested a diel periodicity with an evening minimum for $\rho(NO_3^-)$ but no pattern for $\rho(NH_4^+)$ (Fig. 6-5B,C).

Day-rate estimates of integrated (0-8 m) DIC transport obtained from a single 24 h incubation were 8-21% less than those made by summing results from serial 6 h exposures (Table 6-1). Similar comparisons for depth-integrated values of $\rho_m(NH_4^+)$ indicated that 24 h experiments underestimated daily activity by 23-32%. The data were more variable for NO_3^- as 24 h incubations involved an underestimate (7%) in one instance and overestimates (5 and 14%) in two. Thus, calculated factors, F, for equating results of 24 h exposures to day-rate approximations of depth-integrated DIC and maximum NO_3^- and NH_4^+ transport were 1.16 ± 0.09, 0.97 ± 0.10 and 1.40 ± 0.09.

There were no depth-dependent systematic deviations from depth-integrated F within each experiment and, as stated earlier, no apparent time-dependent, vertical shifts in the algal standing crop. These observations lend credibility to the use of an average F (i.e. invariant with depth) in estimating integral day-rates of

Table 6-1. Comparison of depth-integrated estimates of dissolved inorganic carbon (DIC) and maximum NO_3^- and NH_4^+ transport on a daily basis ($nmol \cdot m^{-2} \cdot d^{-1}$), Toolik Lake phytoplankton. For each time-series experiment, one estimate was derived by summing results of four consecutive 6 h incubations while a second was obtained by a single 24 h exposure. Also given is the factor, F, necessary to equate the day-rate approximation of transport from a 24 h incubation to the superior estimate from several 6 h incubations.

Expt.	Date	Nutrient	(a) Sum, 4x6 h incubations (±SD)	(b) Single 24 h incubation (±SD)	b/a (±SD)	Factor F (±SD)
D1	1 Jul 80	DIC	7140 (162)	6384 (169)	0.89 (0.13)	1.12 (0.04)
		NO_3^-	901 (38)	1030 (100)	1.14 (0.12)	0.88 (0.09)
		NH_4^+	3002 (119)	2053 (196)	0.68 (0.07)	1.46 (0.15)
D2	18 Jul 80	DIC	5016 (102)	3984 (115)	0.79 (0.03)	1.26 (0.04)
		NO_3^-	384 (12)	356 (17)	0.93 (0.05)	1.08 (0.06)
		NH_4^+	1420 (38)	978 (56)	0.69 (0.04)	1.45 (0.09)
D3	5 Aug 80	DIC	8850 (127)	8136 (451)	0.92 (0.05)	1.09 (0.06)
		NO_3^-	295 (10)	309 (18)	1.05 (0.07)	0.95 (0.06)
		NH_4^+	1095 (31)	843 (37)	0.77 (0.04)	1.30 (0.07)

DIC and DIN transport from 24 h experiments.

Overall, the data from time-series analyses showed a strong relationship between PAR and depth-integrated DIC and maximum NO_3^- transport only (Table 6-2). The periodicity in $\rho(NO_3^-)$, surmised by inspection of Fig. 6-5B, was not supported by statistical analysis of depth-integrated data.

Results of time-course experiments (Fig. 6-6) corroborated well those from time-series. Single-factor ANOVA (variances homogeneous for all experiments; F_{max} test) and SNK showed that duration of incubation was of no consequence in calculating mean hourly $V_m(NO_3^-)$ from 4 or 6 to 24 h (Fig. 6-7). In contrast, data for $V_m(NH_4^+)$ showed that short (2-4 h) incubations would yield average hourly values significantly higher than those of longer duration, with some indication of a further decrease in uptake for experiments >18 h.

When V_ms at 6 h were scaled to 24 h and divided by day-rate observations to obtain *F*, resulting values were 1.41 and 1.45 for NH_4^+ and 1.02 and 1.33 for NO_3^- in IT1 and IT2, respectively. All values but the last are in good agreement with time-series data (Table 6-1).

The usual criticisms of 24 h incubations in productivity determinations include respiratory loss of incorporated label (Eppley and Sharp 1975), photoinhibition (Harris and Piccinin 1977) and increased mortality of contained organisms (Gieskes et al. 1979). These are apparently inapplicable here as full day incuba-

Table 6-2. Spearman's rank correlation (r_s) analysis between incident photosynthetically active radiation (PAR) and depth-integrated transport rates for dissolved inorganic carbon (DIC), NO_3^- and NH_4^+ at ambient and transport-saturating nutrient levels in time-series experiments, Toolik Lake. NS = not significant ($P>0.05$; df = 4, all cases).

		Spearman's rank correlation coefficient (r_s)				
		Ambient nutrient levels			Transport-saturating levels	
Expt.	Date	DIC	NO_3^-	NH_4^+	NO_3^-	NH_4^+
D1	1 Jul 80	0.94	NS	NS	0.89	NS
D2	18 Jul 80	0.89	NS	NS	0.94	NS
D3	5 Aug 80	1.00	NS	NS	NS	NS

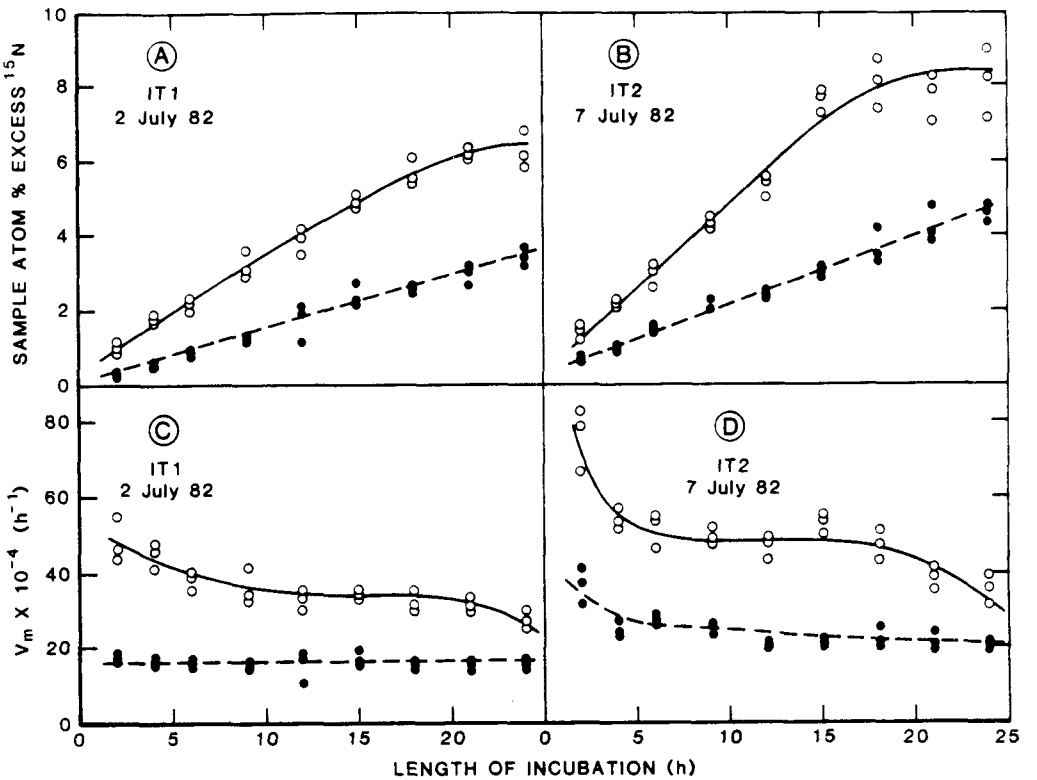

Fig. 6-6. Time-courses for substrate-saturated uptake of NO_3^- and NH_4^+, Toolik Lake phytoplankton, when irradiance and temperature were held constant. (A) and (B) show temporal increases in atom-% excess ^{15}N in the particulate fraction. (C) and (D) give variations in average hourly rates of substrate-saturated uptake (V_m) with length of incubation. Solid (NH_4^+) and broken (NO_3^-) curves fit by eye to highlight trends in data.

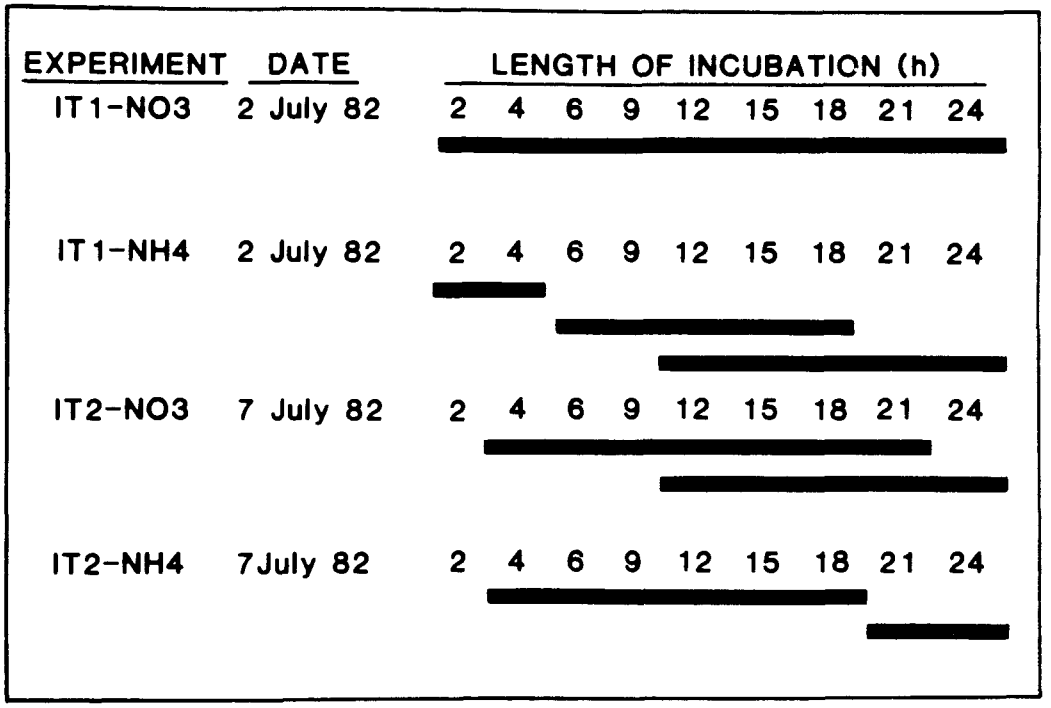

Fig. 6-7. Results of Student-Newman-Keuls test ($P<0.05$) assessing variations in average hourly rates of substrate-saturated uptake of NO_3^- and NH_4^+, Toolik Lake phytoplankton, as a function of duration of incubation in time-courses. Average hourly rates of uptake for lengths of incubation not underscored by same line are significantly different; those underscored by same line are not significantly different.

tions underestimated integral productivity by only 13±7% (Table 6-1). Other arctic investigators have arrived at the same conclusion for Toolik (Miller et al., unpublished manuscript) and Char (Kalff and Welch 1974) lakes.

Day-length incubations for NO_3^- transport in Toolik are also free of deleterious effects. Time-series (Table 6-1) and time-course (Fig. 6-6A,C, Fig. 6-7) analyses indicated linearity of transport (uptake) from ca. 4-24 h, while shorter exposures displayed the well-documented (Goldman and Glibert 1983) "surge uptake" following addition of a critical nutrient.

Linearity in $V_m(NO_3^-)$ also suggests that the reduction in $V_m(NH_4^+)$ after about 18 h (Fig. 6-6B,D, Fig. 6-7) was not due to "other limitation" (e.g. Dugdale et al. 1981). Furthermore, simple calculations reveal that isotope dilution cannot account for this decline. Therefore, it must be due to control by the rate of incorporation into macromolecules or excretion of previously incorporated label.

Experiments lasting several hours unquestionably measure an integrated anabolic response (Wheeler et al. 1982; Berman et al. 1984) as opposed to simple transport across the plasmalemma. Nonetheless, I can correctly state only that I have assessed the latter. The more complex pathway for NO_3^- than NH_4^+ utilization (Syrett 1981) probably diminished the chances of tracer excretion and saturation of assimilative capacity for this nutrient. Thus, in contrast to NH_4^+, uptake was linear from 4-24 h.

For a given incubation period, decreases in V_m at 5 and 8 m reflected the influence of suboptimal light and temperature. Normalization of V_m to the surface water temperature with a Q_{10} of 2.4 (Chapter 4) displaces the 5 and 8 m curves upward in Fig. 6-3 (not shown). Furthermore, these depths correspond to <5% of surface PAR where a light dependence of V_m has been demonstrated (Chapter 4).

Because ρ was back-calculated from ρ_m (V_m) and K_t (Equation 2-1), the similarity between Fig. 6-3 and Fig. 6-5 is not surprising. In fact, if biomass and nutrients remained invariant, corresponding features would coincide exactly between figures as ρ would derive from simply multiplying ρ_m by a scalar. In addition, the significant correlations between depth-integrated transport for NO_3^- at substrate saturation (Table 6-2) would be conferred to transport at ambient conditions. Thus, unlike data for $\rho(C)$ which unequivocally show entrainment to the daily high-low PAR regime (Fig. 6-5A, Table 6-2), these data cannot be used to make conclusive statements concerning circadian rhythmicity of *in situ* DIN transport.

Although back-calculation from 24 h enhanced rates with an experimentally determined F may place undue emphasis on physical factors (PAR, temperature), it probably represents the best estimate of day-rate transport of DIN under ambient conditions. MacIsaac and Dugdale (1972) found for shorter incubations good agreement between back-calculated ρ and values determined directly by limiting $DI^{15}N$ additions to 10% of ambient ^{14}N of the same form.

In addition, Axler et al. (1982) reported remarkable consistency between similarly extrapolated and ^{13}N-determined $\rho(NO_3^-)$. This approach also avoids violation of assumption (b) in tracer studies (see above). Finally, because of their length, these experiments assess assimilation into biomass, the measure of importance when reconciling seasonally chemical and biological budgets for DIN (Chapter 8).

Analysis of the consequences of alternative methods (i.e. extrapolation from short incubations, small enrichments or both) reinforces my choice of technique for estimating daily DIN transport. At characteristic nutrient levels in Toolik it was impossible to satisfy assumption (a) and any attempt would have involved incubations of such brevity (i.e. minutes) that the capabilities of my instrumentation would have been exceeded, assumption (b) would have been breached, or both. Moreover, measured rates would have most closely approximated surge membrane transport only (no assimilation) and extention to day-rate activity simply by scaling measured values (e.g. Kanda et al. 1985) would have been tenuous at best.

CHAPTER 7. SEASONAL TRANSPORT OF DIC AND DIN BY PHYTOPLANKTON

Introduction

Chapters 4-6 explore, at least in part, potential forcing functions for DIN transport and therefore provide the finer details of autotrophic utilization in Toolik Lake. Here, I want an overview. Thus, repeated depth profiles for DIC and DIN transport were obtained with the aim of estimating total seasonal activity, cognizant of the constraints imposed by inadequacies of current experimental techniques (Chapter 6). Secondary goals included (a) assessment of phytoplankton nutritional status through standard but indirect measures (C/N transport ratios, kinetic experiments, relative preference indices and turnover times) and (b) identification of ecological adaptations for efficient function in this N-poor environment.

Methods

Vertical profiles of DIC and DIN transport were taken at roughly 10 d intervals during the mid-May through August sampling seasons of 1980 and 1981. At 0600 local time, water was drawn from five or six depths to a point 2 m beyond the estimated bottom of the euphotic zone (defined here as the depth of 0.5% surface PAR penetration) and ^{14}C or transport-saturating ^{15}N was dispensed into appropriate containers. Bottles were suspended at the depth of sample collection for 24 h. Measured $\rho(C)$ at each depth was adjusted to a day-rate with an F of 1.16 (Chapter 6). Transport

rates for DIN at ambient levels were back-calculated from measured nutrient levels, measured maximum transport rates, $K_t s$ obtained from 4 h kinetic experiments proximate to each profile and Equation 2-1. At each depth, day-rates for $\rho(NH_4^+)$ were approximated by applying an F of 1.4, while data for $\rho(NO_3^-)$ were considered to estimate correctly daily activity without adjustment (Chapter 6).

The exact bottom of the euphotic zone (z_e) was calculated from the relationship $z_e = 5.3(\eta^{-1})$ where η was the measured extinction coefficient. Values for biological (ρ, Chl a) and chemical (NO_3^-, NH_4^+ and PN) variables at z_e were computed by linear interpolation between the most proximal data above and below z_e. Euphotic zone estimates of nutrients (Σ[N]) and Chl a (Σ Chl), as well as day-rate estimates of transport ($\Sigma\rho$) were made by volume weighting the data and normalizing to 1 m^2 lake surface. Expansion over time gave seasonal estimates of weighted, area-based transport ($\Sigma\Sigma\rho$).

Weighted turnover times (TT) and relative preference indices (RPI) for NO_3^- in the euphotic zone were calculated as

$$(7\text{-}1) \qquad TT(NO_3^-) = \frac{\Sigma[NO_3^-]}{\Sigma\rho(NO_3^-)} \qquad \text{and}$$

$$(7\text{-}2) \qquad RPI(NO_3^-) = \frac{\Sigma\rho(NO_3^-)/\Sigma\rho(DIN)}{\Sigma[NO_3^-]/\Sigma[DIN]} \,,$$

where all parameters are as previously defined. Turnover times and

RPIs for NH_4^+ were computed analagously, with NH_4^+ replacing NO_3^- above.

Results and Discussion

In most kinetic experiments, NO_3^- and NH_4^+ transport were Michaelian (Table 7-1). Half-saturation constants for NO_3^- and NH_4^+ ranged from 0.05-0.30 and 0.05-0.49 $\mu mol \cdot L^{-1}$, on the same order as ambient nutrient levels, which ranged from 0.04-0.15 and 0.12-0.32. Overall mean K_ts for NO_3^- (0.11$\pm$0.08) and NH_4^+ (0.15$\pm$0.13) were not significantly different (Student's t-test; df=18).

For the eight dates where matching data were available (Table 7-1), $\rho_m(NH_4^+)$ was significantly higher than $\rho_m(NO_3^-)$ (Paired t-test; df=7), indicating a greater capacity for NH_4^+ transport. The wide range of total data for $\rho_m(NO_3^-)$ and $\rho_m(NH_4^+)$ (factors of ca. 16 and 10, respectively) stems from temporal differences in biomass and temperature. Thus, $\rho_m \cdot Chl^{-1}$ equated to 10°C with a Q_{10} of 2.3 (Chapter 4) varied over factors of 5 and 4 for NO_3^- and NH_4^+ (Table 7-1). These data reflect inherent differences among phytoplankton assemblages and experimental error only.

Highest biomass (Chl *a*) was found in the spring, at 0-1 m beneath the ice bottom (Fig. 7-1A). Immediately following ice-out in both years Chl *a* was evenly distributed at 2.5-3.0 $\mu g \cdot L^{-1}$. However, as the lake stratified thermally in 1980 a metalimnetic maximum developed (Fig. 7-1B). This originated as a sharp peak at 5 m in early July and progressed to a broad 4-6 m band extending

Table 7-1. Kinetic parameters for NO_3^- and NH_4^+ transport, Toolik Lake phytoplankton. Values of the half-saturation constant K_t ($\mu mol \cdot L^{-1}$) and maximum transport rate ρ_m ($nmol \cdot L^{-1} \cdot h^{-1}$) calculated by direct, least-squares fit of Michaelis-Menten equation to transport-concentration data. Also given are the water temperature (°C), chlorophyll-specific maximum transport rate $\rho_m \cdot Chl^{-1}$ ($nmol\ N \cdot \mu g\ Chl^{-1} \cdot h^{-1}$), and $\rho_m \cdot Chl^{-1}$ equated to 10°C with a temperature coefficient (Q_{10}) of 2.3.

		Kinetic parameters				$\rho_m \cdot Chl^{-1}$		$\rho_m \cdot Chl^{-1}$ equated to 10°C	
		NO_3^--N		NH_4^+-N					
Date	Temp.	K_t	ρ_m	K_t	ρ_m	NO_3^-	NH_4^+	NO_3^-	NH_4^+
20 Jun 80	4	*	*	0.05	4.4	-	2.7	-	4.8
6 Jul	13	0.25	9.5	0.49	17.1	4.0	7.3	3.3	6.1
16 Jul	15	0.12	3.0	0.17	5.7	2.7	5.2	1.9	3.7
7 Aug	10	0.07	3.3	0.15	6.2	2.8	5.0	2.8	5.0
21 Aug	9	0.10	2.1	*	*	1.5	-	1.7	-
4 Sep	5	0.30	0.6	0.11	1.8	0.4	1.2	0.7	2.0
5 Jun 81	3	0.05	4.8	*	*	0.9	-	1.7	-
12 Jun	5	0.04	1.8	0.15	5.5	1.5	4.6	2.5	7.6
9 Jul	7	0.06	4.4	0.06	6.4	1.7	2.5	2.4	3.5
28 Jul	14	0.09	4.6	0.08	10.0	3.8	8.3	2.9	6.4
11 Aug	12	0.10	3.3	0.09	7.8	3.0	7.1	2.7	6.3
16 Aug	10	0.07	2.6	*	*	2.2	-	2.2	-

*Data apparently do not conform to Michaelis-Menten kinetics.

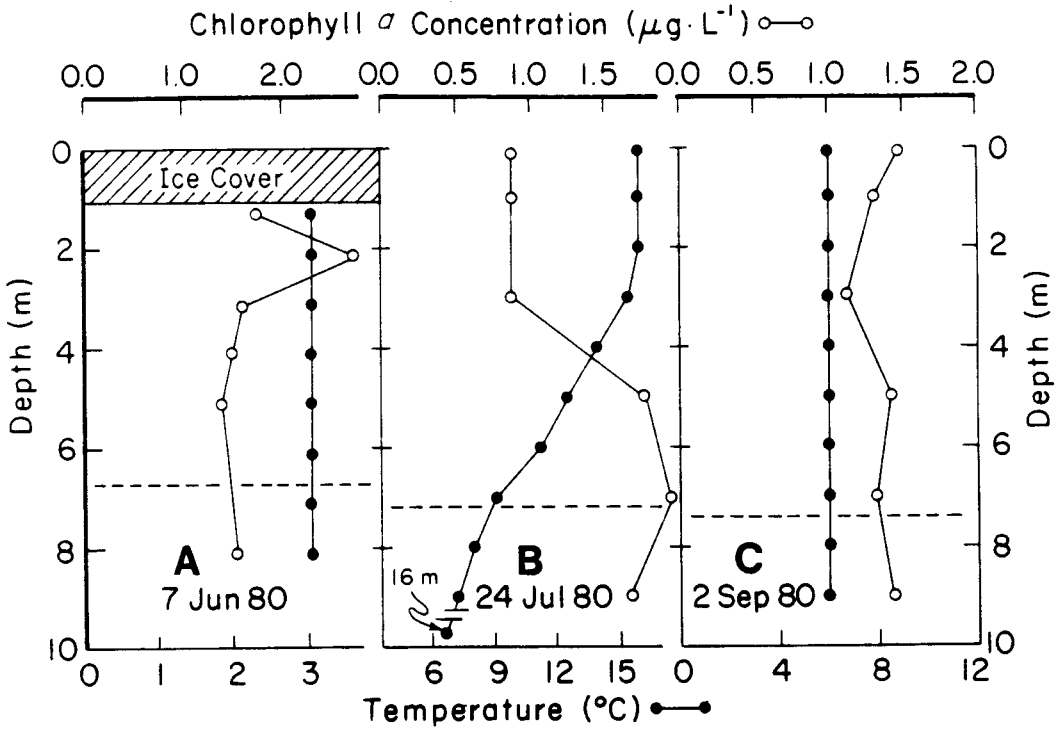

Fig. 7-1. Typical euphotic profiles for chlorophyll *a* and temperature, Toolik Lake. (A) Beneath ice cover in spring; (B) During mid-summer; (C) In the fall. Lower limit of euphotic zone indicated by horizontal broken line and ice cover to scale.

into the hypolimnion. Thermocline erosion in mid-August produced orthograde Chl *a* profiles which persisted through the sampling season (Fig. 7-1C). In 1981 thermal stratification was less well-developed (Fig. 5-2) and a deep Chl *a* maximum was evident on a single date only (23 July). Euphotic distributions were otherwise homogeneous in the open water season.

Transport rates for DIC were always highest at 0-1 m, but decreased to z_e. This pattern held even when $\rho(C)$ was normalized to Chl *a*. Despite markedly higher spring levels of nutrient (Fig. 3-2A), $\rho(NO_3^-)$ at all times was less than $\rho(NH_4^+)$ at a given depth, by as much as a factor of 10 (Fig. 7-2). Vertical profiles for $\rho(NO_3^-)$ and $\rho(NH_4^+)$ varied with biomass and nutrient concentration. As a rule, ρ(DIN) was greatest in the upper half of the euphotic zone, but $\rho(NH_4^+)$ at z_e was sometimes substantial, as much as 65% of near surface values (Fig. 7-2C).

As expected from Chapter 3, $\Sigma[NO_3^-]$ showed striking seasonal changes (Fig. 7-3A,B). The sharp increase between the first two sampling dates of each year reflects the rapid descent of z_e (Table 7-2). With ice-out, $\Sigma[NO_3^-]$ quickly decreased to a relatively unchanging 0.3 mmol$\cdot$m^{-2}. In comparison, $\Sigma[NH_4^+]$ varied little during this investigation (Fig. 7-3A,B).

Seasonally, ΣChl increased from the initiation of sampling to a maximum just after ice-out, decreased continuously to late July and remained constant thereafter to the fall (Fig. 7-3C,D). At all times $\Sigma\rho(C)$ closely tracked ΣChl (Fig. 7-3C,D). Data for $\Sigma\rho(NO_3^-)$

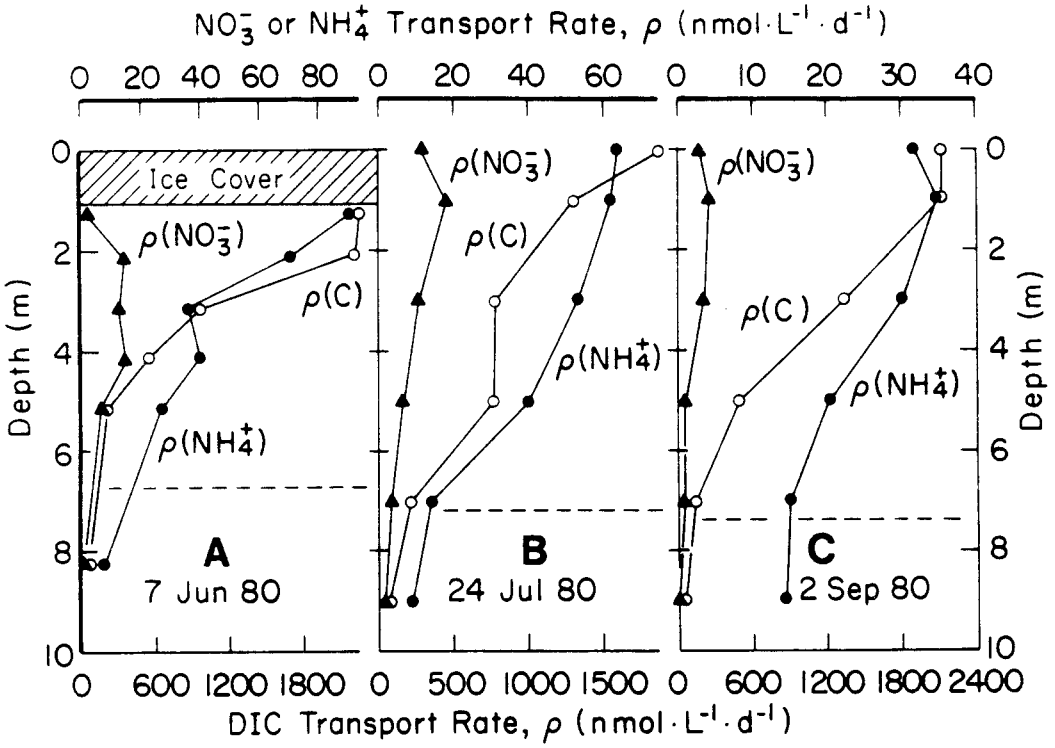

Fig. 7-2. Representative euphotic profiles of *in situ* transport for NO_3^-, NH_4^+ and dissolved inorganic carbon, Toolik Lake phytoplankton. (A) Beneath ice cover in spring; (B) During thermal stratification in mid-summer; (C) After fall overturn. Lower limit of euphotic zone indicated by broken horizontal line and ice cover to scale.

Table 7-2. Seasonal variations in some physical and area-based biological characteristics of Toolik Lake euphotic zone, 1980 and 1981. Included are euphotic depths (z_e, in meters), turnover times (TT, in days), relative preference indices (RPI), dissolved inorganic carbon transport rates ($\Sigma\rho(C)$, in $mmol \cdot m^{-2} \cdot d^{-1}$), chlorophyll-specific rates of dissolved inorganic nitrogen transport ($\Sigma\rho(DIN)/\Sigma Chl$, in $nmol\ N \cdot \mu g\ Chl^{-1} \cdot d^{-1}$), and molar ratios of dissolved inorganic carbon to nitrogen transport at ambient ($\Sigma\rho(C)/\Sigma\rho(DIN)$) and transport-saturating ($\Sigma\rho(C)/\Sigma\rho_m(DIN)$) levels of DIN.

Date	z_e	TT		RPI		$\Sigma\rho(C)$	$\Sigma\rho(DIN)/\Sigma Chl$	$\Sigma\rho(C)/\Sigma\rho(DIN)$	$\Sigma\rho(C)/\Sigma\rho_m(DIN)$
		NO_3^-	NH_4^+	NO_3^-	NH_4^+				
22 May 80	1.8	36	2.0	0.16	3.0	2.02	78	13.6	9.7
29 May	5.9	93	3.8	0.24	6.1	4.91	55	21.8	16.8
7 Jun	5.7	85	3.6	0.21	4.9	3.81	33	17.5	12.6
24 Jun	6.1	10	2.3	0.36	1.6	12.51	31	35.9	23.1
1 Jul	7.7	2.7	1.7	0.80	1.0	5.31	44	10.9	23.3
18 Jul	7.5	6.6	2.0	0.32	1.0	3.26	81	7.2	3.1
24 Jul	7.2	4.5	2.5	0.63	1.2	4.57	52	15.6	6.4
5 Aug	8.0	2.9	1.7	0.68	1.2	7.04	59	17.7	7.4
10 Aug	6.4	4.2	2.7	0.74	1.2	6.47	54	20.7	10.5
19 Aug	7.2	9.4	4.4	0.56	1.2	6.70	48	22.4	13.2
2 Sep	7.4	35	5.8	0.21	1.4	6.05	24	40.6	22.2
3 Jun 81	3.4	24	1.5	0.43	6.8	5.50	58	21.2	21.2
10 Jun	5.3	62	4.9	0.36	4.6	4.59	71	13.7	10.0
6 Jul	6.3	2.3	2.0	0.92	1.0	10.40	35	23.7	14.4
14 Jul	8.0	1.8	1.8	1.00	1.0	6.90	50	12.1	7.6
23 Jul	7.1	2.3	1.9	0.83	1.0	5.04	133	7.0	4.6
30 Jul	8.0	3.7	2.8	0.81	1.0	5.02	84	9.0	6.1
8 Aug	8.7	2.8	1.5	0.64	1.1	3.87	143	5.1	3.0
15 Aug	9.3	4.9	3.6	0.81	1.0	3.83	63	10.3	6.4
25 Aug	8.4	2.5	2.6	1.00	1.0	5.91	60	13.3	7.6

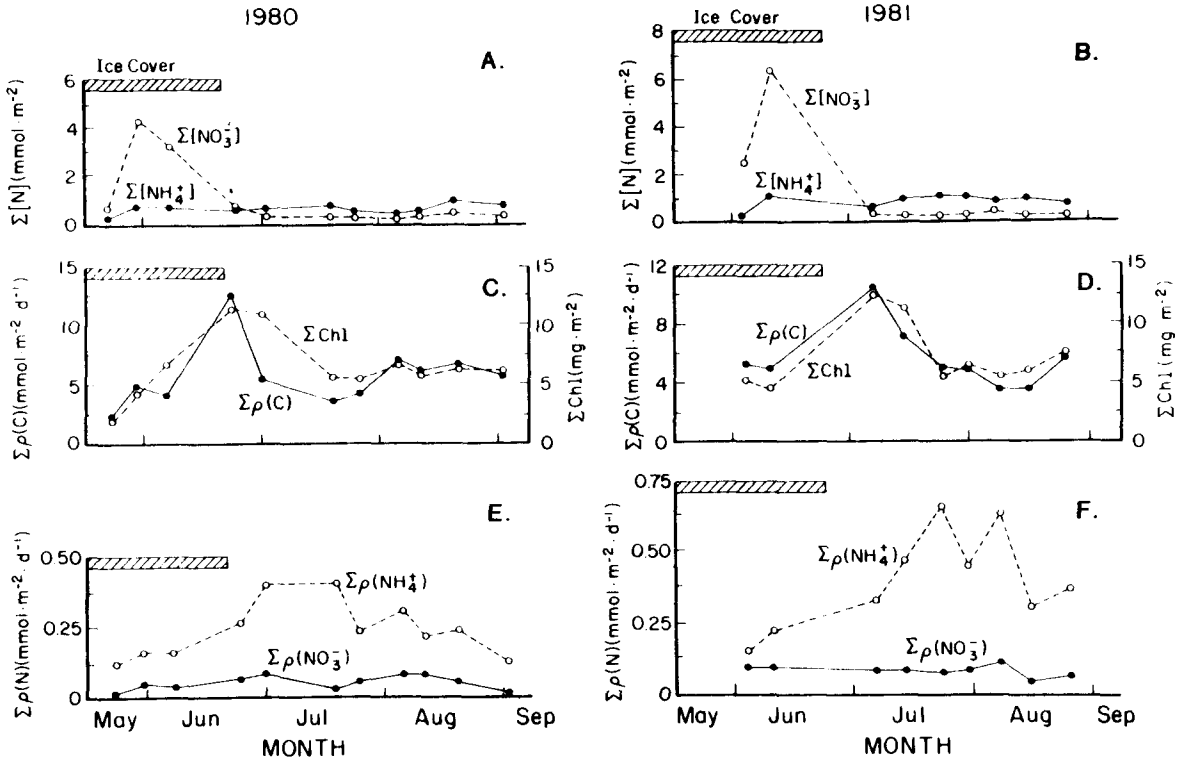

Fig. 7-3. Seasonal variations in area-based euphotic variables, Toolik Lake. (A,B) Ambient NO_3^- and NH_4^+ (Σ[N]); (C,D) Phytoplankton chlorophyll a (ΣChl) and dissolved inorganic carbon transport ($\Sigma\rho$(C)); (E,F) Dissolved inorganic nitrogen transport by phytoplankton ($\Sigma\rho$(N)).

showed little seasonal variability, while that for $\Sigma\rho(NH_4^+)$ had a maximum in July or July-August (Fig. 7-3C,D).

All data for $\Sigma\rho$ are slight underestimates of whole lake activity due to continued transport below z_e, especially for NH_4^+ (Fig. 7-2C). Small lake volumes in deep strata minimized this error. Calculation of $\Sigma\rho$ from surface to bottom profiles in 1979 (n=6) indicated that on the average 2±2, 4±3 and 7±2% of transport for DIC, NO_3^- and NH_4^+ occurred below 8 m (z_e averaged 7.6 m for the ice-free portions of 1980 and 1981; Table 7-2).

Turnover times (Table 7-2) for NH_4^+ were virtually constant at 2-3 d throughout the study while those for NO_3^- were notably higher in the spring than later in the year (exception: 2 September 1980). The difference between overall means for NO_3^- (19.8±28.4 d) and NH_4^+ (2.8±1.2) was significant (Student's t-test; df=19). However, for the ice-free period the difference (6.3±8.3, NO_3^-; 2.6±1.2, NH_4^+) was not significant (Student's t-test; df=14).

In the relative preference index of McCarthy et al. (1977), a value of unity indicates NO_3^- and NH_4^+ transport equitable with availability while lesser and higher values denote rejection and preferential utilization. RPIs consistently showed an early season selection against NO_3^- and for NH_4^+ (Table 7-2). This trend was relaxed for the ice-free portion of 1980 and the open-water season of 1981 was characterized by approximately balanced transport and availability for both DIN species.

Low ambient DIN led to high DIC/DIN transport ratios (mol),

with the average for the entire study being 17.0±9.1 (Table 7-2). The contrasting mean at transport-saturating levels of DIN was 32% lower, 11.5±6.7.

Euphotic DIN transport was 34 and 41 $mmol \cdot m^{-2}$ during the 1980 and 1981 investigative periods, with NO_3^- transport comprising <20% of the total (Table 7-3). Comparison of these and data for substrate-saturated transport indicated that *in situ* activity was 42 (1980) and 62% (1981) of the theoretical maximum. Inorganic carbon transport was 622 and 504 $mmol \cdot m^{-2}$ for the respective sample years, giving molar ratios of 18.3 and 12.3 for DIC/DIN transport. Corresponding ratios at transport-saturating levels of DIN were 7.6 and 7.7.

The subsurface Chl *a* maximum found at a low PAR level, in or below a pronounced thermocline in 1980 has also been reported under similar conditions for a multitude of north temperate lakes (Moll et al. 1984). In the lone arctic observation, Kalff et al. (1972) noted a seasonally shifting vertical pattern for Chl *a* in response to the light climate alone in unstratified Char Lake.

The 1980 data for DIC transport (Table 7-3) are my most extensive but probably underestimate annual activity by about 15%, based on spatially (above) and temporally broader data from 1979. Thus, annual phytoplankton production in Toolik is roughly two times the 340 $mmol \cdot m^{-2}$ given by Kalff and Welch (1974) for Char Lake. This difference probably stems from Toolik's warmer temperature (maximum in Char is 4.5°C; Schindler et al. 1974a), longer ice-free season

Table 7-3. Seasonal summaries of area-based transport ($mmol \cdot m^{-2}$) for dissolved inorganic nitrogen (DIN) and carbon at ambient ($\Sigma\Sigma\rho$) and transport-saturating ($\Sigma\Sigma\rho_m$) levels of DIN, Toolik Lake euphotic zone. Also included are molar C/DIN transport ratios at ambient ($\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho(DIN)$ and transport-saturating ($\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho_m(DIN)$) levels of DIN.

Variable	22 May-2 Sep 1980	3 Jun-25 Aug 1981
$\Sigma\Sigma\rho(NO_3^-)$	6	8
$\Sigma\Sigma\rho(NH_4^+)$	28	33
$\Sigma\Sigma\rho(DIN)$	34	41
$\Sigma\Sigma\rho(C)$	622	504
$\Sigma\Sigma\rho_m(NO_3^-)$	21	17
$\Sigma\Sigma\rho_m(NH_4^+)$	60	49
$\Sigma\Sigma\rho_m(DIN)$	81	66
$\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho(DIN)$	18.3	12.3
$\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho_m(DIN)$	7.7	7.6

(about 1 mo in Char; Kalff and Welch 1974) and greater external nutrient loading rate (comparison in Chapter 3). Nonetheless, Toolik certainly ranks among the least productive of water bodies examined (compendium in Westlake 1980).

The data for DIN transport and kinetics point to a phytoplankton community during the ice-free period well-adapted for life in an N-poor environment. Values for $K_t(NO_3^-)$ and $K_t(NH_4^+)$ (Table 7-1) are the lowest reported for fresh waters and the lack of statistical significance between means indicates a strong affinity for both DIN species. During the open-water season the proximity of RPIs to 1.0 for both DIN species (Table 7-2) and the lack of a significant difference between mean TTs for NO_3^- and NH_4^+ point to a high demand for and lack of discrimination between these two forms of nutrient.

Despite physiological suitability to their surroundings, available evidence indicates N deficiency in the phytoplankton. McCarthy (1981) suggested that RPIs for NO_3^- and NH_4^+ will converge on unity (Table 7-2) as DIN concentrations begin to restrict algal growth. Additionally, comprehensive ratios for DIC/DIN transport (Table 7-3) were 2-3 times higher than the Redfield ratio of 6.5 for N-replete algal biomass.

A curious anomaly in the phytoplankton ecology of Toolik is the apparent inability of spring populations to utilize effectively the overwinter accumulation of NO_3^- (Fig. 3-2A). Water column profiles for NO_3^- showed a net loss of 5.4 $mmol \cdot m^{-2}$ during 7-24 June

1980, of which only about 0.3 and 1.0 were accounted for by riverine export and flux to the phytoplankton. Moreover, my confidence in the latter value is high because $\rho(NO_3^-)$ at >1 m beneath the ice was unconstrained by substrate concentration and hence free of potential errors from back-calculation.

In the early season, an elevated $\rho_m(NO_3^-)\cdot Chl^{-1}$ would be clearly advantageous. This adaptation was absent, however, as comparison of means for temperature-normalized (Q_{10}=2.3; Chapter 4) $\Sigma\rho_m(NO_3^-)/\Sigma Chl$ during the ice-covered (40±14 nmol N·µg $Chl^{-1}\cdot d^{-1}$) and ice-free (32±13) seasons revealed no significant differences (Student's t-test; df=18). This is reinforced in the limited data where temperature-normalized $\rho_m(NO_3^-)\cdot Chl^{-1}$ from 7-12 June 1981 (lake ice-covered) falls within the range for the open water period (Table 7-1). Thus, beneath ice cover, the usual regulator of nitrate transport (ambient concentration) was supplanted by not only physical controls (PAR, temperature), but by an intrinsic factor as well.

Benthic autotrophs may have provided a sink for early season NO_3^-. G. Kipphut (Inst. Mar. Sci., Univ. AK, pers. comm.) found for the 1-5 m zone in Toolik epipelic production of 5 mmol $C\cdot m^{-2}\cdot d^{-1}$ while Yeakel (1977) reported annual epilithic production to be 33 mmol $C\cdot m^{-2}$ lake surface. Assuming a 125 d growing season and a lake bottom of 75% soft sediment (Hershey and McDonald 1985), I calculate annual benthic productivity to be about 500 mmol $C\cdot m^{-2}$. Inasmuch as Kipphut's measurements did not encompass the entire

euphotic zone, they err on the low side, suggesting that benthic and pelagic productivity are approximately equal. By proportionality, then, the benthic NO_3^- flux would be 1.0 $mmol \cdot m^{-2}$, but only about 43% of the total loss would then be accounted for. However, Axler et al. (1984) reported that benthic algae were remarkably more active in NO_3^- transport than their planktonic counterparts following epilimnetic NH_4NO_3 fertilization of an oligotrophic lake. The same may be true here for the early season.

In summary, these data point to a highly unproductive pelagic ecosystem with spring phytoplankton incapable of exploiting elevated NO_3^- and summer assemblages stressed for N, but well-adapted to utilizing efficiently limit of detection NO_3^- and NH_4^+.

CHAPTER 8. FUNCTION OF THE PELAGIC ECOSYSTEM: COMPARISON OF BIOLOGICAL AND CHEMICAL BUDGETS FOR DIN

Introduction

The purpose of this chapter is to extend the trophodynamic concept of new and regenerated phytoplankton primary production from marine systems to Toolik Lake. My efforts focus on the period of stream flow for 1980 which began on 13 May, terminated on about 15 September and probably encompassed nearly all of the growing season for the phytoplankton (Chapters 3 and 7).

By assuming that PN is autochthonously-derived and new production results only from NO_3^- utilization (Eppley and Peterson 1979), nutrient fluxes have been reduced to an important few and new and regenerated primary biosynthesis have been evaluated for a variety of marine waters. These data indicate that the ratio of new/total primary production increases both with increasing total production and proximity to land (Eppley and Peterson 1979; Harrison 1980).

Control over nutrient supply also varies along an offshore gradient. In oceanic waters, diffused and upwelled NO_3^- stimulate new production (roughly 10-20% of total), while epilimnetic recycling maintains the quasi-steady state standing crop (Eppley and Peterson 1979). Shoreward, benthic recycling may provide about 50% of the phytoplankton N requirement (Harrison 1980; Blackburn and Henricksen 1983; Boynton and Kemp 1985). Horizontally-advected (currents) nutrients may augment or supplant local upwelling and eddy diffusion as a driving force behind new production (Eppley and

Peterson 1979; Harrison et al. 1983; Sambrotto et al. 1984).

For all but the largest and deepest of lakes or those with closed basins, surface water flows represent prominent gain and loss terms for nutrients. More importantly, this invalidates the simplifying supposition that NO_3^- transport alone adequately defines new production.

The complexity introduced by riverine input and other potentially important fluxes (e.g. loss to benthic algae) has perhaps discouraged limnologists from similarly modelling lacustrine systems and further, almost demands that such endeavors be restricted to a semiquantitative nature. In the single attempt to date, Axler and Gersberg (1981) showed that oligotrophic Castle Lake functioned in a manner similar to unproductive oceanic regions as new production in the euphotic zone was < 5-36% of the total. However, for the summer period of measure, external inputs were small and new biosynthesis was presumed to be due entirely to NO_3^- accumulated in the spring or diffused from aphotic water.

Clearly, from reviews of marine studies (Eppley and Peterson 1979; Harrison 1980), physically and geographically heterogeneous environments display variable dependence on a few logical avenues of nutrient supply to the phytoplankton. In contrast, for most lacustrine waters, individuality guarantees unpredictability. In particular, for Toolik, the high area of sediment-water contact argues for a benthic-pelagic coupling as in coastal waters. On the other hand, the low level of phytoplankton productivity (Chapter 7)

is characteristic of the open ocean and suggests a reduced particulate load to the sediment with correspondingly low benthic remineralization. Moreover, in the absence of N-fixation, the low riverine concentration of nutrients but short water renewal time (Chapter 3) represent the major opposing and interacting forces that must set the ratio of new/total production somewhere along the generalized marine scale showing an increase with increasing eutrophy (i.e. shoreward progression).

The cumulative, indirect evidence for N deficiency in Toolik phytoplankton (Chapters 5 and 7) ensures that meaningful information will result from any success in this first approximation of a comprehensive understanding of driving forces behind pelagic productivity therein.

Methods

Information presented here was extrapolated or taken directly from that given in earlier chapters with one exception. An overwinter experiment measuring the potential for nitrification was conducted with aphotic (16 m) samples from 28 October 1980 through 10 June 1981. Water was collected into a 20-L carboy to which $^{14}NO_3^-$ (10 $\mu mol \cdot L^{-1}$) and $^{15}NO_3^-$ (2 $\mu mol \cdot L^{-1}$) were added. The contents were mixed and distributed into eight 4-L containers which were subsequently amended with variable concentrations (0-15 $\mu mol \cdot L^{-1}$) of $^{14}NH_4^+$ and returned to the depth of collection. Overwinter nitrification was assessed by isotope dilution following NO_3^-

extraction according to Schell (1978).

For the investigative period, I have generally considered that measurements made at the index station were representative of the lake as a whole, the rate of DIN regeneration in the water column for 1980 was similar to that recorded for 1981, the lake functioned as a single, well-mixed box and a dynamic steady state existed with respect to DIN flux to the lake waters and phytoplankton.

The latter two assumptions can be challenged on the grounds that Toolik stratified thermally for 5-6 wk (Fig. 5-2) and NO_3^- was elevated in the spring (Fig. 3-2A). However, during thermal stratification the mixed layer eventually exceeded the lake's mean depth (Fig. 5-2), hypolimnetic nutrient storage was nil (Fig. 3-2B) and $\Sigma\Sigma\rho(NO_3^-)$ was <20% of $\Sigma\Sigma\rho$(DIN) for the phytoplankton (Table 7-3). These observations affirm the general validity of my suppositions. Specific assumptions will be invoked as necessary.

Results and Discussion

Data from Table 3-3 were extended to 15 September assuming a constant nutrient load from 31 August (last day of measure) onward. Comparison of Table 3-3 and Table 8-1 suggests that riverine fluxes after the 1980 sampling season were small. By similarly extrapolating early and late season measurements to 13 May and 15 September and correcting for transport below z_e (Chapter 7), data from Table 7-3 were used to estimate DIN transport for the period of stream flow, $\Sigma\Sigma\rho'$ (Table 8-2).

Table 8-1. Nitrogen fluxes for Toolik Lake during the period of stream flow in 1980, 13 May through 15 September. All values as $mmol \cdot m^{-2}$ lake surface.

Parameter	Stream inflow	Direct precipitation	Total input	Stream outflow	Net (in-out)	% input retained
Nitrate-N	3.2	0.5	3.7	1.3	2.4	64
Ammonium-N	3.4	0.2	3.6	2.4	1.2	33
Dissolved organic-N	261	2.0	263	213	50	18
Particulate-N	29.4	3.6	33.0	35.3	-2.3	-7
Total-N			303	252	51	17

Table 8-2. Supply and phytoplankton transport of dissolved inorganic nitrogen (DIN = NO_3^- + NH_4^+) in Toolik Lake, 13 May-15 September 1980. All values as mmol·m^{-2} lake surface. Values in parentheses are percent contribution to phytoplankton DIN transport.

Flux term	NO_3^-	NH_4^+	DIN
Net allochthonous input	2.4	1.2	3.6 (9)
Sediment release	-	3.9-7.5	3.9-7.5 (10-19)
Pelagic recycling	-	25.8-42.2	25.8-42.2 (66-108)
Total supply	2.4	30.9-51.2	33.3-53.6 (85-137)
Phytoplankton transport	6.1	33.0	39.1

Unfortunately, the fate of the riverine PN input (Chapter 3) is not tractable. Additionally, phytoplankton use of DON (i.e. DON flux to PN fraction; unquantified here) may be as much as 50% of $\rho(NH_4^+)$ (Eppley 1981). In concert, these confound estimation of the rate of DIN supply through water column regeneration.

A first approximation of this pelagic recycling rate was derived in Chapter 3 by comparison of the PN flux to the sediment with the autochthonous formation of PN from DIN alone, assuming all or none of the allochthonous PN input settled. A better indication of the short-term destiny of the external PN load and, hence, rate of local recycling in Toolik is gained from sediment trap studies in lakes with minimal or no allochthonous inputs. These have demonstrated that 19% of PN (Kimmel and Goldman 1976) and 27-30% of particulate organic carbon (POC) production (Kimmel and Goldman 1976; Lastein 1976; Andersen et al. 1979) reached the sediment surface.

By assuming that autochthonous PN production in Toolik resulted from DIN or DIN + DON (i.e. NO_3^- + 1.5 NH_4^+) assimilation and that all of the external PN input settled, I calculate that for 1981 24-34% of autochthonously-derived PN reached the sediment with 66-76% recycled in the water as NH_4^+. This is in good agreement with the fractional sediment flux from closed basin lacustrine studies and marine observations that pelagic NH_4^+ remineralization and transport are essentially in balance (Caperon et al. 1979; Glibert 1982). This also corroborates well the general tenet that

particulate organic matter (POM) of terrigenous origin decomposes 1-2 orders of magnitude slower than autochthonously-derived POM (Saunders 1980). Finally, it is consistent with my qualitative observation that filter-trapped particulates in Toolik inflows were large enough to be visible to the naked eye (i.e. settled rapidly and had an unfavorable surface/volume ratio for microbial attack), unlike those from the lake outflow.

Consequently, in approximating the contribution of local recycling to the phytoplankton DIN supply in 1980 (Table 8-2) I have assumed that the entire allochthonous PN input reached the lake bottom with boundary conditions of autochthonous PN formation from DIN or DIN + DON. Any mineralization of river-borne PN was presumed to occur following sedimentation and was thus accounted for in the sediment efflux.

The ^{210}Pb and overwinter DIN accumulation data (Chapter 3) project directly to a flux from the sediment of 3.9-7.5 $mmol \cdot m^{-2}$ DIN for the 1980 growing season (Table 8-2). The former technique provides no information concerning the form of DIN released, while data from the latter indicate pelagic recharge with NO_3^-. Nonetheless, I have assumed that DIN was liberated as NH_4^+. The relative proportions of NO_3^- and NH_4^+ in DIN released from the sediment reflect the net result of biological and diffusive processes. In summer benthic chamber experiments for the Toolik eulittoral zone Kipphut (pers. comm.) found daily rates of internal loading of 0.05-0.10 $mmol \cdot m^{-2}$, totally as NH_4^+. In the absence of phytoplank-

ton activity during the polar night, nitrification may dominate sediment DIN transformations (ignoring denitrification). In the summer, epipelic algae likely intercept upwardly diffusing NO_3^- and release reduced forms of N (NH_4^+, DON) from catabolic processes.

If 75% of the lake bottom is soft sediment (Hershey and McDonald 1985), the midrange of Kipphut's data extrapolate to a release of 7.0 $mmol \cdot m^{-2}$ DIN for the 125 d under discussion, in remarkable concordance with the 7.5 calculated from overwinter accumulation (Table 8-2). Although agreement may be coincidental based on the above, it is close enough to the ^{210}Pb approximation to add confidence to my estimated internal loading rate.

The total NH_4^+ supply is reasonably consistent with $\Sigma\Sigma\rho'(NH_4^+)$, but NO_3^- supply is only about 40% of $\Sigma\Sigma\rho'(NO_3^-)$ (Table 8-2). A portion of the necessary NO_3^- may derive from overwinter accumulation (Fig. 7-3A), but the relative constancy of $\Sigma\rho(NO_3^-)$ (Fig. 7-3E) suggests a continuous pelagic supply during the summer. Unmeasured fluxes that would increase the NO_3^- input include water column nitrification as well as diffusion from the profundal sediment (27% of lake area at depth >10 m) where benthic algae are excluded. Recent evidence for marine systems (Ward 1982) shows that NH_4^+-oxidizing bacteria in the water are several orders of magnitude more abundant than previously thought and in one instance accounted for 30% of total (bacterial + algal) NH_4^+ utilization (Priscu and Downes 1985).

Linear regression of atom-% excess $^{15}NO_3^-$ against $^{14}NH_4^+$ gave a

significant (df=6) and negative slope in the isotope dilution experiment, indicating at least qualitatively that water column nitrification was operative here. Stoichiometric oxidation of NH_4^+ to NO_3^- (i.e. no accumulation of intermediary metabolites) in Toolik waters would improve agreement between supply and demand for both DIN forms (Table 8-2).

At face value, the data from Table 8-2 indicate that pelagically recycled nutrients, the sediment regenerative flux and allochthonous input provided about 66-108, 10-19 and 9% of the phytoplankton DIN demand. Thus, the data suggest that Toolik functions most like the oligotrophic ocean, except the meager nutrient supply fueling new primary production derives from horizontally-advected (riverine) input rather than from vertical transfer of bathyal reserves.

This analysis, however, ignores primary productivity by at least the epilithic fraction of the benthos which may alter the allochthonous and pelagic recycling components of DIN supply to the phytoplankton (sediment efflux term already accounts for benthic activity). Resource partitioning would increase the "goodness of fit" between supply and phytoplankton demand for DIN because the former was probably somewhat in excess of the latter (Table 8-2).

Inclusion of the benthic component does not seriously jeopardize the argument that the pelagic ecosystem of Toolik operates largely on locally recycled nutrient, like the oligotrophic ocean. However, other considerations imply extensive

use of another source of new N and, hence, function in a manner more analagous to coastal waters with respect to new/total productivity.

Adhering to previously defined suppositions (above and Chapter 7), $\Sigma\Sigma\rho'(C)$ from 13 May through 15 September was 733 $mmol \cdot m^{-2}$, giving a DIC/DIN transport ratio of 18.7. For two dates when simultaneous profiles were available, the volume-weighted ratio of POC/PN (POC data from Cornwell 1983) for the lake was 12.3 ± 0.1. This discrepancy between ratios for seston and transport can be effected in three ways: (a) the overwhelming influence of allochthonous particulates, (b) respiratory loss of fixed DIC and (c) phytoplankton utilization of DON.

Options (a) and (b) likely had a minor impact because the gross allochthonous PN input to the lake (which probably sedimented rapidly) was less than the autochthonous flux via DIN (cf. Table 8-1, Table 8-2) while respiratory loss of photoassimilated DIC was probably small and accounted for by F (Chapter 7).

Alternative (c) is most likely based on three lines of evidence. First, the lake showed a net gain of 50 $mmol \cdot m^{-2}$ DON (Table 8-1). Second, if DON use was as extensive as Eppley (1981) suggests (supported by preliminary analysis of my unpublished urea-N transport experiments for Toolik in 1983), $\Sigma\Sigma\rho'$ for total dissolved nitrogen (TDN) was about 56 $mmol \cdot m^{-2}$. This would decrease the C/N transport ratio to 13.2, in close agreement with that for the seston. The DON flux to the phytoplankton would be 17

$mmol \cdot m^{-2}$, with utilization by benthic autotrophs representing an additional unassessed sink. Third, there is considerable evidence that the Toolik watershed can act as a source of assimilable DON (at least amino acids) for the lake phytoplankton. Sowden et al. (1977) reported that for a variety of arctic zones 33±9% of the hydrolyzable component of total soil N consisted of amino acids while Kielland (unpubl. data) showed that water extractable (easily leached) amino acids comprised 4.8±2.2% of the soluble organic N in soils of the Toolik watershed. These may be readily mobilized and transported to Toolik inlets during storms, considering the shallow active layer of the tundra.

The capacity of phytoplankton to utilize directly many simple organic-N compounds is well-documented for laboratory cultures, but availability and exploitation (beyond urea-N) in natural waters are poorly understood (Bonin and Maestrini 1981; Paul 1983). Nonetheless, cumulative indirect evidence suggests that this fraction of TDN is an important nutrient source for oligotrophic marine waters (Jackson and Williams 1985).

The intractability of allochthonously-derived DON and PN, lack of data for ρ(DON) and the chemical nature of allochthonous DON, as well as the inability to validify estimated day-rates of phytoplankton activity render my semiquantitative model of ecosystem function impossible to prove or disprove. Appreciable utilization of autochthonous DON or water column degradation of riverine PN and DON can undermine the model. Nonetheless, it is

tenuously supported by the consistency between biological and chemical mass balances for DIN in conjunction with indirect observations (e.g. sestonic POC/PN values). Moreover, the inference of extensive phytoplankton assimilation of allochthonous DON, drawn from the combined chemical and biological data, is no different than would be derived simply from the N budget of Chapter 3, but is more firmly based.

Although my attempt to quantify sources of new and regenerated N for Toolik phytoplankton was minimally successful due to the complexity of the system, several conclusions can be drawn from the data. First, benthic-pelagic coupling in N supply to pelagic waters was less than expected based on the high area of sediment-water contact. This was a direct consequence of the low nutrient content of the watershed and lake which kept lacustrine productivity small. Second, new primary production may have been greater than the 9% calculated from the DIN supply-demand balance. New biosynthesis could be driven by horizontally-advected DON and may account for as much as 35% of $\Sigma\Sigma\rho'$(TDN) if DON was utilized at 50% of the rate for NH_4^+ and was derived exclusively from external loading. Third, the data emphasize the importance of simultaneously analyzing chemical and biological budgets for N in lacustrine studies of new and regenerated primary production. This is especially important when many major fluxes are not satisfactorily tractable and standard marine assumptions are invalid. Last, this study adds to the growing body of circumstantial and

direct evidence pointing to phytoplankton reliance on DON as a major nutrient source in N-impoverished aquatic systems.

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APPENDIX A. DATA FROM CHAPTER 2.

Data in this appendix include:

(1) Comparison of pump- and Van Dorn-collected surface water samples with regard to ^{14}C (dpm) and ^{15}N (atom-% excess) incorporation into the particulate fraction.

(2) Comparison of Gelman A/E glass fiber and 0.45-μm Millipore nitrocellulose filters in retaining particle-bound ^{14}C (dpm).

(3) Calibration of Bendix 17-210 mass spectrometer using reagent grade NH_4Cl (natural abundance) and phthalimide of known ^{15}N content.

(4) Estimates for precision of NO_3^-, NH_4^+ and dissolved organic nitrogen analyses (all as $\mu mol \cdot L^{-1}$).

Comparison between submersible pump and Van Dorn sampler, 8/28/80

^{14}C		$^{15}NO_3^-$		$^{15}NH_4^+$	
Pump	Van Dorn	Pump	Van Dorn	Pump	Van Dorn
10788	12112	1.03	1.19	2.39	1.48
11705	11056	0.79	1.18	2.20	2.34
11075	11618	0.74	1.13	1.67	1.86
10425	12217	0.78	1.14	1.96	2.01
12437	10784	1.20	1.04	3.33	3.19
11654	11711	1.23	0.70	2.96	3.33
12806	10367	1.19	0.70	3.15	3.10
12038	10445	1.23	0.74	3.38	3.15
11205	10663	1.28	1.14	2.68	3.29
11754	12146	1.22	1.23	3.01	3.71

Calibration of Bendix mass spectrometer (atom % ^{15}N), 7/16/82

NH_4Cl	C_6H_4-CONHCO			
Natural abundance	Known	Measured		
0.40	1.02	1.04	1.06	0.99
0.35	4.00	3.89	3.85	3.92
0.35	7.00	6.67	7.10	7.19
0.38	10.02	10.27	9.59	9.75
0.37	15.03	14.42	14.05	14.20
0.33	25.03	21.32	22.48	22.92

Precision of NO_3^-, NH_4^+ and dissolved organic nitrogen (DON) analyses

NO_3^-		NO_4^+		DON
8/15/80	8/28/81	8/15/80	8/28/81	7/12/82
0.05	0.08	0.04	0.12	16.9
0.05	0.11	0.04	0.13	16.9
0.05	0.06	0.05	0.17	17.5
0.04	0.06	0.04	0.17	16.9
0.05	0.08	0.06	0.15	16.9
0.05	0.05	0.04	0.13	16.9
0.04	0.11	0.04	0.13	17.2
0.05	0.05	0.05	0.12	17.5
0.05	0.06	0.04	0.12	17.5
0.05	0.08	0.04	0.16	16.9

Retention of ^{14}C by filters, 8/14/80

Gelman A/E	0.45 µm Millipore
14047	12223
13374	12477
14403	12721
14402	11967
14262	13349
13808	12310
13715	12920
13909	13850
12362	12005
13314	12037

APPENDIX B. DATA FROM CHAPTER 3.

Data in this appendix include:

(1) Depth profiles for NO_3^-, NH_4^+, DON and PN (all as μmol $N \cdot L^{-1}$).

(2) Stream water concentrations for NO_3^-, NH_4^+, DON and PN (all as μmol $N \cdot L^{-1}$).

(3) Concentrations of NO_3^- and NH_4^+ in precipitation (all as μmol $N \cdot L^{-1}$).

(4) Fluxes of PN to sediment (μmol $N \cdot m^{-2} \cdot d^{-1}$).

Data for DIN transport rates by phytoplankton appear in Appendix F and stream flow volumes are in Cornwell (1983).

Depth profiles for NO_3^-, 1980

Depth (m)	5/20	5/22	5/27	5/29	6/03	6/05	6/07	6/22	6/24	7/01	7/04	7/18
0								0.27	0.10	0.03	0.05	0.06
1	1.03	0.03	0:16	0.05	0.04	0.05	0.02	0.27	0.06	0.03	0.05	0.04
2		0.50	0.84	1.14	0.62	1.48	0.17					
3	1.49	0.77	0.75	1.39	1.43	2.14	1.33	0.17	0.20	0.03	0.05	0.07
4				1.39	1.34	2.07	1.49					
5	1.88	1.02	1.59	1.29	1.19	2.10	1.01	0.22	0.19	0.03	0.04	0.08
6												
7								0.25	0.22		0.04	
8	2.79	1.64	1.41	1.34	1.33	1.52	1.38			0.08		0.14
9												
10								0.24	0.30		0.07	
12	3.33		2.62	1.15		1.31		0.23		0.07		
16	3.29			2.40		3.07		0.52				

Depth (m)	7/21	7/24	7/30	8/05	8/10	8/17	8/19	8/21	8/31	9/02	10/28
0	0.05	0.04	0.07	0.04	0.05	0.05	0.08	0.08	0.05	0.06	
1	0.05	0.06	0.00	0.04	0.14	0.06	0.07	0.09	0.08	0.08	0.17
2											
3	0.05	0.05	0.05	0.05	0.07	0.07	0.12	0.08	0.08	0.08	0.21
4											
5	0.05	0.05	0.07	0.06	0.05	0.07	0.12	0.07	0.08	0.09	0.18
6											
7	0.06	0.06	0.05		0.11	0.08	0.15	0.06	0.09	0.08	
8				0.07							0.35
9	0.09	0.08	0.06		0.12	0.07	0.12	0.07	0.07	0.07	
10											
12	0.09			0.13		0.05			0.07		0.24
16	0.10			0.13		0.05			0.07		0.42

Depth profiles for NH_4^+, 1980

Depth (m)	5/20	5/22	5/27	5/29	6/03	6/05	6/07	6/22	6/24	7/01	7/04	7/18
0								0.19	0.15	0.14	0.17	0.17
1	0.20	0.10	0.22	0.20	0.17	0.00	0.14	0.17	0.15	0.14	0.16	0.17
2		0.23	0.20	0.21	0.19	0.24	0.16					
3	0.17	0.12	0.15	0.20	0.20	0.23	0.18	0.22	0.15	0.14	0.14	0.16
4				0.15	0.20	0.22	0.17					
5	0.15	0.11	0.13	0.15	0.19	0.19	0.21	0.24	0.15	0.14	0.18	0.17
6												
7								0.20	0.15		0.21	
8	0.14	0.14	0.08	0.14	0.19	0.18	0.17			0.13		0.18
9									0.15			
10								0.19			0.19	
12	0.14		0.10	0.15		0.19		0.15		0.13		
16	0.13			0.14		0.19		0.12				

Depth (m)	7/21	7/24	7/30	8/05	8/10	8/17	8/19	8/21	8/31	9/02	10/28
0	0.10	0.13	0.18	0.08	0.14	0.19	0.19	0.16	0.14	0.15	
1	0.09	0.13	0.16	0.09	0.14	0.19	0.18	0.17	0.14	0.17	0.21
2											
3	0.11	0.13	0.13	0.09	0.14	0.20	0.23	0.20	0.13	0.17	0.27
4											
5	0.11	0.11	0.18	0.06	0.13	0.19	0.28	0.16	0.13	0.16	0.23
6											
7	0.12	0.10	0.17		0.13	0.22	0.27	0.20	0.12	0.15	
8				0.06							0.34
9	0.17	0.13	0.22		0.15	0.23	0.24	0.19	0.13	0.13	
10											
12	0.20			0.16		0.27			0.14		0.38
16	0.22			0.20		0.28			0.14		0.31

Depth profiles for NO_3^-, 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			0.03	0.03	0.04	0.06	0.06	0.06	0.05
1	0.06	0.07	0.04	0.03	0.04	0.09	0.05	0.04	0.03
2	0.07	0.07	0.05	0.03					
3	1.35	2.79	0.05	0.04	0.03	0.07	0.07	0.03	0.03
4	2.28	2.93							
5	1.60	2.67	0.06	0.03	0.04	0.07	0.05	0.04	0.03
7	3.03	2.70			0.04	0.04	0.07	0.05	0.03
8			0.06	0.04					
9					0.04	0.04	0.08	0.05	0.03
12	4.98	5.17	0.05	0.04	0.04	0.09	0.05	0.04	0
16	6.11	6.17	0.07	0.03	0.04	0.08	0.11	0.04	0.03

Depth profiles for NH_4^+, 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			0.08	0.24	0.26	0.07	0.12	0.15	0.14
1	0.04	0.25	0.08	0.15	0.27	0.14	0.11	0.14	0.14
2	0.14	0.33	0.07	0.13					
3	0.03	0.30	0.21	0.17	0.25	0.29	0.20	0.18	0.14
4	0.13	0.32							
5	0.14	0.40	0.27	0.18	0.28	0.29	0.20	0.34	0.30
7	0.18	0.19			0.29	0.41	0.25	0.22	0.20
8			0.13	0.17					
9					0.31	0.40	0.26	0.20	0.24
12	0.29	0.18	0.15	0.17	0.35	0.48	0.40	0.36	0.28
16	0.28	0.19	0.27	0.16	0.38	0.47	0.40	0.39	0.14

Depth profiles for DON, 1980

Depth (m)	5/20	5/25	5/29	6/05	6/22	7/01	7/21	8/04	8/17	8/30
0					10.9	15.0	16.0	16.0	15.0	17.0
1	19.0	13.4	18.3	11.9	14.0	15.0	17.0	16.0	15.0	16.0
3	16.8	14.9	30.1	18.6	15.0	15.5	15.0	16.5	16.0	15.5
5	17.7	17.1	17.7	18.6	14.9	16.0	14.0	16.0	15.0	12.5
7					14.3		15.0		17.0	15.5
8	19.0	16.2	18.4	29.2		16.0		16.5		
9									15.0	16.0
12	18.6	18.4	17.4	19.1	10.9	15.5	15.0	16.0	16.0	15.0
16	19.3	19.9	21.1	20.6	15.3		15.0	16.0	18.1	15.5

Depth profiles for DON, 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			8.4	6.6	11.2	11.0	11.6	12.8	5.0
1	14.6	14.0	7.8	20.8	10.0	9.5	11.3	11.3	10.1
3	7.5	16.5	9.7	10.3	10.3	10.7	11.0	11.3	10.4
5	6.9	30.1	8.4	9.7	16.2	10.7	10.7	11.6	10.4
7		15.9			10.9	7.1	10.7	10.7	7.4
8	15.2		10.3	12.1					
9					11.2	9.8	10.7	10.4	7.4
12	16.2	14.6	7.5	7.8	11.5	11.0	11.3	17.5	3.5
16	16.5	14.0	8.4	12.1	11.5	11.3	11.6	11.6	7.4

Depth profile for PN (±SD), 1980

Depth (m)	5/20	5/22	5/27	5/29	6/05	6/07	6/22	6/24	7/01	7/04
0							1.8 (0)	1.9 (0.3)	2.7 (0.1)	1.6
1	1.5 (0.2)	1.5 (0.3)	3.5 (0.2)	2.5 (0.1)	2.5 (0.5)	2.1 (0.1)	2.4 (0.1)	1.9 (0.3)	2.5 (0.2)	1.7 (0.2)
2		4.8 (0.6)	6.0 (0.2)	1.8 (0.4)	1.7 (0.1)	1.8 (0)				
3	1.1 (0.1)	1.7 (0.6)	2.2 (0.2)	1.2	1.0 (0)	1.7 (0.1)	2.6 (0.1)	2.0 (0.2)	3.3 (0.6)	2.1 (0.6)
4				2.0 (0.2)	1.6 (0.4)	1.9 (0.3)				
5	0.8 (0)	1.0 (0)	1.1 (0)	1.6 (0.1)	2.1 (0.7)	1.7 (0.2)	2.7 (0.2)	2.4 (0)	4.1 (0.9)	2.8 (0.4)
6										
7							2.4 (0)	1.7 (0.2)		2.3 (0.3)
8	0.9 (0.1)	1.2 (0.4)	0.7 (0)	1.4 (0.4)	1.1 (0.3)	1.4 (0)			3.2 (1.0)	
9										
10							3.0 (0.5)	1.5 (0.1)		1.4 (0.2)
12	0.9 (0.2)		0.6 (0.1)	0.7 (0)	1.0		2.9 (0.3)		2.1 (0.2)	
16	1.4 (0.1)			0.7 (0.1)	0.7 (0.1)		2.2 (0.2)		2.8 (0.4)	

Depth (m)	7/18	7/21	7/24	8/05	8/10	8/17	8/19	8/31	9/02
0	1.7 (0.2)	1.5	1.1 (0.1)	2.1 (0.3)	1.6 (0.1)	1.5 (0)	1.8 (0.1)	1.4 (0)	1.7 (0.1)
1	1.7 (0.2)	1.3 (0.1)	1.2 (0.1)	1.9 (0.1)	1.4 (0.1)	1.3 (0.1)	1.6 (0.1)	1.5 (0.2)	1.5 (0)
2									
3	1.7 (0.1)	1.9 (0.2)	1.2 (0.2)	1.7 (0)	1.3 (0)	1.3 (0.1)	1.5 (0.1)	1.7 (0.1)	1.3 (0.1)
4									
5	2.1 (0.1)	1.9 (0.2)	1.4 (0.1)	1.7 (0)	1.2 (0.1)	1.6 (0.2)	1.4 (0.1)	2.1 (0.2)	1.1 (0.1)
6									
7		1.9 (0.3)	1.2 (0.1)		1.4 (0.6)	1.7	1.4 (0.2)	1.6 (0)	1.3 (0.1)
8	2.7 (0.2)			1.6 (0.2)					
9		1.6 (0.2)	1.2 (0.1)		1.4 (0.1)	1.6 (0.2)	1.3 (0)	1.6 (0.1)	1.7 (0.3)
10									
12		1.4 (0.2)		1.8 (0.2)				1.5 (0)	
16		1.2 (0.1)		1.7 (0.1)				1.9 (0.2)	

Depth profiles for PN (±SD), 1981

Depth (m)	6/03	6/11	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			2.7 (0.1)	2.6 (0.3)	1.6 (0.4)	1.4 (0.3)	3.0 (0.1)	1.4 (0.1)	1.6 (0.1)
1	4.0	4.1 (0.4)	2.7	2.2	1.5 (0.1)	1.7 (0)	2.1 (0.3)	1.5 (0.1)	2.0 (0.1)
2	8.7 (1.4)	2.7 (0.2)	2.8 (0.3)	2.1 (0.1)					
3	3.8 (0.5)	1.9 (0)	2.7 (0)	2.1 (0.1)	1.9 (0.1)	1.9 (0)	1.8 (0.3)	1.6 (0.1)	1.6 (0.2)
4	1.5 (0.1)	1.8 (0)							
5	1.6 (0)	1.8 (0.2)	2.4 (0.1)	2.5 (0)	2.1 (0.2)	1.7 (0.1)	1.9 (0.1)	1.8 (0.4)	1.9 (0.3)
6									
7	2.0 (0.3)	1.9 (0.2)			1.9 (0.1)	1.5 (0.4)	2.5 (0.4)	1.7 (0.1)	2.1 (0.4)
8			3.0 (0.9)	2.5 (0.1)					
9					1.7	1.5 (0.1)	1.7 (0)	1.8 (0.6)	1.8 (0.1)
12	1.2 (0.3)	1.4 (0.2)	2.7 (0.1)	2.3 (0.1)	1.9 (0.2)	1.5 (0.1)	2.0 (0.3)	1.4 (0.1)	1.7 (0.1)
16	1.5 (0.2)	1.3 (0)	2.9 (0)	2.3 (0.3)	1.8 (0.1)	1.6 (0.1)	2.1 (0.3)	1.5 (0)	2.0 (0)

Stream water chemistry for 1980

	Inlet 1				Inlet 2				Outlet			
Date	NO_3^-	NH_4^+	DON	PN	NO_3^-	NH_4^+	DON	PN	NO_3^-	NH_4^+	DON	PN
5/14	0.15	0.60	39.9	5.9					-	-	-	-
5/16	-	-	30.0	5.4					1.00	0.25	18.2	4.4
5/18	0.11	0.67	27.3	4.9					1.02	0.28	21.2	-
5/21	0.20	0.46	28.0	4.3					0.73	0.26	24.2	4.3
5/25	0.30	0.24	21.4	3.5	0.11	0.26	32.0	5.6	0.44	0.23	23.9	4.5
5/27	0.28	0.18	27.2	3.8	0.42	0.20	17.0	2.8	0.30	0.24	27.2	3.9
5/30	0.07	0.17	15.5	2.7					0.03	0.17	16.0	4.0
6/03	0.08	0.17	15.0	2.6					0.03	0.16	15.0	4.0
6/08	0.06	0.22	18.0	2.9					0.06	0.16	14.5	4.1
6/16	0.00	0.24	17.6	2.2	0.10	0.19	14.5	1.9	0.21	0.21	16.0	3.2
6/23	0.13	0.27	35.8	1.3	0.07	0.22	13.0	0.9	0.17	0.15	15.5	3.4
6/29	0.42	0.25	14.0	1.8					0.03	0.21	12.5	3.6
7/05	0.03	0.29	18.0	1.7	0.03	0.27	13.0	1.3	0.03	0.21	14.5	2.1
7/13	0.20	0.25	16.5	1.4					0.05	0.22	15.5	2.2
7/20	0.91	0.19	15.0	1.7					0.05	0.13	14.5	2.0
7/27	0.39	0.08	14.5	1.5					0.05	0.08	15.5	2.2
8/03	0.59	0.14	16.5	1.6					0.00	0.14	15.5	2.0
8/18	0.31	0.15	16.0	1.2					0.09	0.15	15.0	2.0
8/23	0.86	0.14	16.0	1.1					0.10	0.14	16.0	2.0
8/30	0.59	0.14	15.5	1.2					0.12	0.13	15.0	2.4

Stream water chemistry for 1981

	Inlet 1				Inlet 2				Outlet			
Date	NO_3^-	NH_4^+	DON	PN	NO_3^-	NH_4^+	DON	PN	NO_3^-	NH_4^+	DON	PN
6/02	0.29	0.44	11.5	1.8					0.39	0.06	27.0	3.8
6/08	0.13	0.44	11.5	1.8					0.05	0.26	14.6	3.8
6/13	0.04	0.18	12.8	1.7	0.04	0.23	14.6	2.1	0.05	0.20	11.8	3.4
6/16	0.04	0.17	12.8	1.6	0.06	0.23	13.7	1.5	0.04	0.23	11.8	3.4
6/29	0.06	0.20	11.8	2.5					0.04	0.62	9.7	3.1
7/05	0.06	0.53	22.7	3.0	0.06	0.20	15.9	2.6	0.04	0.20	10.0	3.0
7/10	0.06	0.16	10.3	2.4	0.07	0.16	4.7	1.5	0.08	4.68	16.5	3.7
7/17	0.05	0.19	11.4	1.4	0.07	0.17	8.5	1.5	0.05	0.19	13.8	2.5
7/22	0.09	0.20	12.5	1.3					0.05	0.26	11.2	2.8
7/28	0.06	0.30	6.6	1.5					0.03	0.30	9.4	3.5
8/01	0.13	0.22	12.2	2.0					0.06	0.28	10.1	2.3
8/07	0.46	0.23	12.2	1.6					0.06	0.27	11.0	1.9
8/11	0.05	0.23	12.8	1.8	0.06	0.23	12.2	1.1	0.03	0.17	10.7	1.5
8/18	0.08	0.21	12.2	2.5					0.05	0.07	12.2	3.5
8/29	0.18	0.11	12.2	1.2					0.06	0.12	10.7	2.0

Precipitation data for 1980 and 1981; sediment trap data for 1981

Precipitation						Sediment traps	
	1980			1981			
Date	NO_3^-	NH_4^+	Date	NO_3^-	NH_4^+	Dates	PN (±SD)
6/10*	2.52	0.28	6/07*	3.86	2.56	6/02-6/09	0.36 (0.03)
6/16	1.09	0.49	6/12	0.97	1.22	6/09-6/14	0.19 (0.03)
6/18	0.75	0.23	6/15	5.25	5.36	6/14-7/08	-
6/19	1.01	0.41	7/04	3.11	-	7/08-7/11	0.86 (0.07)
6/22	0.53	0.03	7/05	0.73	6.44	7/11-7/15	0.89 (0.04)
6/26	0.95	0.51	7/07*	0.04	0.41	7/15-7/22	0.44 (0.06)
6/27	0.67	0.39	7/12	0.25	7.34	7/22-7/29	0.43 (0.04)
6/29	0.54	2.71	7/14	0.67	7.36	7/29-8/07	0.36 (0.08)
6/30	4.91	-	7/30	0.15	3.93	8/07-8/11	0.43 (0.02)
7/01	2.22	-	8/10	0.06	1.45	8/11-8/15	0.41 (0.04)
7/02	1.24	1.06	8/13	0.50	3.32	8/15-8/18	0.61 (0.01)
7/03	0.62	1.72	8/15*	0.77	3.63	8/18-8/26	0.31 (0.01)
7/04	-	0.61				8/26-8/29	0.45 (0.18)
7/10	-	0.52					
7/13	0.26	0.83					
7/14	1.05	0.55					

*Data for fresh snow

APPENDIX C. DATA FROM CHAPTER 4.

Data in this appendix include:

(1) Ambient DIN ($\mu mol\ N \cdot L^{-1}$) and Chl *a* ($\mu g \cdot L^{-1}$) levels for temperature and light dependence experiments.

(2) Transport rates for DIN ($nmol\ N \cdot L^{-1} \cdot h^{-1}$) as a function of temperature.

(3) Transport rates for DIN ($nmol \cdot L^{-1} \cdot d^{-1}$) as a function of PAR at 0.25 m.

Chl *a* and NO_3^- transport data for Fig. 4-4 are in Appendix F while nutrient levels for Fig. 4-4 are in Appendix B.

Ambient DIN and Chl *a* (±SD) levels, light and temperature dependence experiments

Expt	Ambient nutrients NO_3^-	Ambient nutrients NH_4^+	Chl *a* (±SD)
T1	0.16	0.16	3.2 (0)
T2	0.04	0.14	1.1 (0)
T3	0.05	0.21	1.2 (0.1)
T4	0.04	0.16	1.5 (0)
LT1	0.05	0.19	1.7 (0.3)
LT2	0.04	0.18	1.2 (0)
LT3	0.04	0.17	1.5 (0)
LT4	0.07	0.31	4.0 (0.8)
LT5	0.04	0.30	1.2 (0)
LT6	0.11	0.13	2.1 (0.1)
LT7	0.06	0.23	1.2 (0)
LT8	0.08	0.26	1.0 (0.1)
LT9	0.03	0.34	1.2 (0)

DIN transport rates, temperature dependence experiments

Expt	Temp	ρ_T (NO_3^-)			ρ_T (NH_4^+)		
T1	4.0	5.1	5.9	5.1	10.0	11.3	10.8
	11.0	10.0	11.6	11.9	19.8	20.0	21.3
	16.0	12.7	14.5	16.1	25.6	27.2	24.6
	22.0	12.4	10.3	10.0	29.4	22.8	26.4
	29.0	2.9	2.9	3.5	10.2	11.0	10.8
T2	3.5	1.3	1.3	1.5	3.3	2.8	2.2
	8.0	1.9	2.0	2.3	4.6	4.7	5.3
	13.5	2.5	2.7	2.6	7.0	7.0	6.7
	20.0	3.7	3.3	4.5	10.7	10.9	11.2
	27.0	2.7	2.9	2.0	9.1	10.5	8.1
T3	4.0	1.3	1.4	1.6	3.7	4.1	4.2
	10.0	3.4	3.0	2.9	8.0	8.5	9.1
	15.0	4.8	6.3	4.1	12.0	11.5	14.4
	21.0	5.3	6.4	6.3	13.1	14.6	15.7
	28.0	3.0	2.5	3.3	12.9	12.4	10.7
T4	4.0	1.0	0.9	0.8	2.1	2.0	2.2
	8.5	1.3	1.6	1.5	3.3	3.0	4.0
	14.0	2.1	2.3	1.9	5.1	5.8	6.0
	20.0	2.3	3.3	4.0	8.1	9.7	7.8
	25.5	1.3	1.5	1.1	7.1	7.4	6.4

DIN transport rates, light dependence experiments

	ρ (NO_3^-) for % PAR at 0.25 m															
Expt	0 (dark)		1.2		6.5		9.3		11.5		25.1		47.9		100 (light)	
LT1	4.9	2.7	7.1	7.1	15.2	14.7	28.7	23.9	25.5	20.1	52.0	43.6	60.4	52.0	69.7	70.7
LT2	13.1	14.7	18.6	18.7	38.9	38.1	72.6	60.8	57.1	55.5	68.2	73.4	79.2	79.3	70.4	57.1
LT3	3.3	3.5	10.1	6.2	16.7	13.9	44.7	30.8	30.9	33.6	48.4	42.0	41.9	46.6	29.9	30.8
LT4	2.7	2.6	9.9	10.8	33.1	31.4	56.1	61.3	54.3	49.0	56.1	57.8	61.3	63.0	42.0	17.1
LT5	5.3	6.5	18.2	15.9	24.0	22.8	24.0	37.8	30.9	15.9	37.8	33.2	52.6	15.8	28.8	25.2
LT6	33.7	39.6	45.5	40.0	70.3	64.5	103	113	96.1	84.7	116	120	122	116	105	107
LT7	27.0	29.7	37.8	45.8	59.0	45.7	88.9	77.9	105	86.4	102	92.3	128	97.4	118	-
LT8	12.2	15.0	15.0	14.1	22.1	21.2	43.3	47.7	33.7	45.1	47.7	54.6	68.3	46.0	89.2	85.9
LT9	9.4	9.0	11.9	15.7	25.6	18.1	56.2	55.0	53.7	50.2	68.2	59.8	89.5	61.0	95.4	95.2

	ρ (NH_4^+) for % PAR at 0.25 m															
Expt	0 (dark)		1.2		6.5		9.3		11.5		25.1		47.9		100 (light)	
LT1	48.8	57.7	78.2	70.7	109	101	130	144	137	141	171	161	163	180	184	-
LT2	65.0	75.1	88.8	84.2	94.9	126	155	130	148	129	166	149	178	128	160	151
LT3	45.6	45.8	54.8	57.7	75.0	69.6	115	106	99	109	105	101	106	118	77.8	89.5
LT4	45.0	45.1	56.4	77.1	116	118	143	110	130	147	132	145	134	154	90	109
LT5	57.7	65.0	71.0	67.4	88.9	78.2	107	103	98.3	71.0	74.6	103	97.1	103	138	104
LT6	110	115	125	120	138	143	199	181	184	177	200	217	207	218	207	226
LT7	107	118	128	110	143	117	213	181	170	209	218	215	197	202	199	196
LT6	66.6	64.8	75.6	90.0	95.3	104	102	134	122	120	151	168	164	177	189	177
LT9	49.4	57.4	77.1	74.5	71.9	96.6	127	125	126	125	142	132	174	148	202	191

APPENDIX D. DATA FROM CHAPTER 5.

Data in this appendix include:

(1) Temperature (°C) profiles for Toolik Lake.

(2) Transport rates ($nmol \cdot L^{-1} \cdot d^{-1}$) for DIC and DIN in bioassay experiments.

Ambient nutrient and Chl *a* levels are in Table 5-1 of the text.

Temperature profiles, 1980

Depth (m)	5/20	5/29	6/07	6/22	6/26	7/01	7/04	7/18	7/24	7/30	8/05	8/10	8/19	8/31	9/02
0				4.5	8.5	13.0	14.0	16.0	12.0	11.0	9.0	10.0	8.5	7.0	6.0
1	1.5	4.5	3.0	5.0	8.5	13.0	14.0	16.0	12.0	11.0	9.5	10.0	8.5	7.0	6.0
2	1.5	3.0	3.0					15.0	14.0	11.0	9.5	10.0	8.5		6.0
3	1.5	3.0	3.0	5.0	8.5	10.5	13.0	14.5	14.0	11.0	9.5	10.0	8.5	7.0	6.0
4	2.0	3.0	3.0					14.0	12.5	11.0	9.5	10.0	8.5		6.0
5	2.0	3.0	3.0	4.5	6.5	9.5	8.0	12.0	11.0	11.0	9.5	10.0	8.5	7.0	6.0
6	2.0	3.0	3.0					10.5	9.0	11.0	9.5	10.0	8.5		6.0
7	2.0	3.0	3.0	4.5	6.5		7.5	10.0	8.0	9.0	9.5	10.0	8.5	7.0	6.0
8	2.5	3.0	3.0			6.0		8.0	8.0		9.0	10.0	8.5		6.0
9	2.5	2.5	3.0					7.5	7.0	7.0	8.5	10.0	8.5	7.0	6.0
10	2.5	2.5	3.0	4.5	6.0		6.0	7.0	7.0		8.0	9.5			
11	2.5	2.5	3.0					6.5	7.0		7.5	8.0			
12	2.5	2.5	3.0	4.5	6.0	6.0		6.5	7.0	7.0	7.0	7.5		6.5	6.0
13	2.5	2.5	3.0					6.5	7.0		7.0	7.0			
14	2.5	2.5	3.0					6.0	7.0		6.5	7.0			
15	2.5	2.5	3.0					6.0	7.0		6.5	6.5		6.5	
16	2.5	2.5	3.0	4.5	5.0	5.0		6.0	6.5	6.5	6.5	6.5		6.5	6.0

Temperature profiles, 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			6.5	8.0	13.0	12.0	12.0	11.0	8.0
1	3.5	4.5	6.5	8.0	13.0	12.0	12.0	10.5	8.0
2	3.5	4.0	6.5	8.0					
3	3.0	3.5	6.5	8.0	12.0	12.0	12.0	10.5	8.0
4	3.0	3.5							
5	3.0	3.5	6.5		11.0	12.0	12.0	10.5	8.0
7	3.0	3.5			10.0	12.0	11.0	10.5	8.0
8			6.5	7.5					
9					9.0	9.5	10.0	10.5	8.0
10			6.5						
12	3.0	3.0	6.5	7.5	8.5	8.5	8.5	8.5	8.0
16	3.0	3.0	6.5	7.5	8.0	8.5	8.5	8.5	8.0

Mean transport rates (±SD) for each treatment in ^{14}C bioassays

Expt	Date	CONT	NH4	NO3	PO4	SALT
P1	7/09/80	1533 (51)	2301 (320)	2441 (186)	1791 (99)	1565 (135)
P2	7/26	475 (59)	682 (152)	542 (36)	572 (88)	407 (54)
P3	8/24	378 (24)	417 (45)	417 (70)	365 (8)	337 (11)
P4	6/07/81	5065 (92)	6826 (541)	7312 (508)	5642 (461)	5464 (325)
P5	6/13	1760 (48)	2343 (46)	2636 (177)	1852 (81)	1872 (158)
P6	7/11	1588 (90)	1992 (221)	1826 (359)	2023 (155)	2309 (133)
P7	7/25	1831 (114)	2543 (270)	2734 (147)	1408 (107)	1822 (64)
P8	8/01	802 (118)	1199 (184)	1080 (119)	667 (195)	727 (163)
P9	8/08	1729 (108)	3009 (147)	2567 (102)	1849 (240)	1783 (98)
P10	8/13	687 (114)	1335 (155)	1230 (98)	726 (147)	822 (170)
P11	8/18	1410 (93)	1968 (32)	1667 (93)	1442 (37)	1370 (27)
P12	8/29	1368 (138)	1661 (115)	1353 (82)	1039 (125)	1169 (100)

Expt	Date	MO	TMEDTA	EDTA	VIT	N+P
P1	7/09/80	1545 (107)	1527 (44)	1711 (295)	1282 (63)	-
P2	7/26	472 (88)	591 (12)	595 (41)	485 (60)	911 (59)
P3	8/24	368 (35)	362 (12)	322 (17)	433 (35)	418 (18)
P4	6/07/81	7159 (267)	3938 (345)	4907 (625)	4763 (691)	6812 (473)
P5	6/13	1977 (138)	1900 (128)	1440 (55)	1665 (77)	2717 (166)
P6	7/11	1629 (47)	1375 (21)	1527 (135)	1285 (81)	2333 (116)
P7	7/25	1967 (93)	1890 (50)	1991 (272)	1835 (288)	3038 (230)
P8	8/01	857 (132)	1084 (83)	1028 (42)	926 (63)	1634 (120)
P9	8/08	1943 (146)	1952 (31)	1608 (193)	1397 (118)	3178 (144)
P10	8/13	783 (158)	981 (105)	906 (151)	639 (79)	1831 (74)
P11	8/18	1444 (175)	1779 (99)	1466 (165)	1355 (42)	2613 (49)
P12	8/29	1163 (112)	1215 (32)	1165 (78)	994 (40)	1630 (53)

Mean transport rates (±SD) for each treatment in $^{15}NO_3^-$ bioassays

Expt	Date	CONT	NH4	PO4	SALT	MO	TMEDTA	EDTA	VIT
P1	7/09/80	173 (6)	30 (5)	244 (25)	183 (22)	183 (14)	187 (16)	191 (12)	185 (20)
P2	7/26	78 (8)	12 (2)	108 (9)	83 (5)	88 (8)	80 (8)	84 (2)	78 (7)
P3	8/24	53 (9)	7 (2)	77 (7)	57 (4)	58 (6)	58 (6)	47 (7)	60 (6)
P4	6/07/81	75 (4)	28 (3)	108 (6)	76 (4)	79 (2)	57 (5)	79 (2)	77 (7)
P5	6/13	46 (6)	6 (2)	29 (2)	43 (2)	49 (2)	41 (3)	9 (2)	43 (4)
P6	7/11	71 (2)	27 (2)	107 (2)	78 (2)	59 (3)	63 (3)	67 (2)	60 (3)
P7	7/25	71 (11)	11 (2)	108 (5)	76 (6)	83 (14)	77 (8)	71 (11)	68 (5)
P8	8/01	68 (5)	19 (2)	99 (11)	68 (6)	74 (2)	76 (6)	80 (8)	83 (6)
P9	8/08	74 (6)	9 (2)	91 (11)	81 (4)	81 (3)	68 (14)	72 (13)	59 (10)
P10	8/13	48 (6)	11 (2)	56 (9)	49 (8)	50 (11)	48 (8)	46 (6)	40 (3)
P11	8/18	73 (3)	14 (2)	90 (15)	66 (6)	76 (10)	76 (3)	71 (10)	81 (13)
P12	8/29	51 (2)	13 (2)	67 (5)	55 (4)	59 (4)	57 (6)	52 (3)	51 (9)

Mean transport rates (±SD) for each treatment in $^{15}NH_4^+$ bioassays

Expt	Date	CONT	NO3	PO4	SALT	MO	TMEDTA	EDTA	VIT
P1	7/09/80	364 (21)	272 (19)	444 (34)	364 (7)	343 (29)	369 (17)	362 (30)	362 (22)
P2	7/26	173 (17)	151 (8)	233 (13)	188 (26)	197 (20)	172 (11)	172 (18)	169 (14)
P3	8/24	110 (6)	90 (5)	157 (18)	115 (6)	102 (11)	103 (12)	98 (14)	106 (6)
P4	6/07/81	149 (9)	152 (9)	212 (3)	162 (2)	176 (6)	145 (4)	168 (6)	163 (14)
P5	6/13	129 (12)	98 (7)	111 (10)	121 (3)	131 (12)	136 (7)	54 (3)	143 (8)
P6	7/11	109 (16)	86 (5)	181 (11)	120 (9)	106 (3)	112 (14)	113 (9)	111 (9)
P7	7/25	159 (14)	123 (9)	214 (20)	171 (13)	176 (13)	175 (7)	161 (18)	176 (11)
P8	8/01	124 (7)	106 (23)	197 (5)	135 (22)	134 (18)	139 (14)	147 (9)	160 (4)
P9	8/08	148 (8)	117 (4)	215 (5)	158 (5)	157 (14)	157 (5)	159 (3)	150 (16)
P10	8/13	97 (9)	78 (16)	119 (10)	106 (9)	102 (10)	102 (14)	100 (10)	97 (19)
P11	8/18	143 (5)	105 (3)	195 (11)	148 (32)	140 (8)	142 (19)	141 (26)	190 (4)
P12	8/29	103 (9)	70 (6)	130 (26)	119 (7)	111 (13)	106 (19)	94 (10)	91 (9)

APPENDIX E. DATA FROM CHAPTER 6.

Data in this appendix include:

(1) Depth profiles for NO_3^-, NH_4^+ and PN (all as $\mu mol\ N \cdot L^{-1}$) during each incubation of time-series experiments.

(2) Depth profiles for $\rho_m(NO_3^-)$, $\rho_m(NH_4^+)$ and $\rho(C)$ (all as $nmol \cdot L^{-1} \cdot h^{-1}$) during each incubation of time-series experiments.

(3) Incident PAR ($\mu E \cdot m^{-2} \cdot s^{-1}$) during each incubation of time-series experiments.

(4) V_m for NO_3^- and NH_4^+ ($X\ 10^{-4} \cdot h^{-1}$) for time-course experiments.

Temperature and kinetic data for time-series experiments are in Appendices D and F. Values of V_m, V and ρ for DIN in time-series can be calculated from data given here and in the text. The ambient nutrient levels for 24 h incubations were considered to be the same as for Incubation 1 in time-series experiments.

Ambient NO_3^-, time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period 1	2	3	4	5	6
D1	1 Jul	0	0.03	0.03	0.03	0.03	0.03	0.04
		1	0.03	0.03	0.03	0.03	0.03	0.03
		3	0.03	0.03	0.03	0.03	0.03	0.03
		5	0.03	0.03	0.03	0.03	0.03	0.03
		8	0.08	0.06	0.03	0.04	0.04	0.03
D2	18 Jul	0	0.06	0.03	0.07	0.07	0.05	0.03
		1	0.04	0.03	0.06	0.07	0.05	0.03
		3	0.07	0.03	0.06	0.07	0.04	0.03
		5	0.08	0.03	0.06	0.06	0.04	0.04
		8	0.14	0.13	0.08	0.09	0.03	0.07
D3	5 Aug	0	0.04	0.04	0.04	0.04	0.04	0.06
		1	0 04	0.04	0.08	0.03	0.04	0.06
		3	0.05	0.05	0.06	0.03	0.04	0.05
		5	0.06	0.05	0.04	0.03	0.04	0.05
		8	0.07	0.08	0.05	0.03	0.06	0.05

Ambient NH_4^+, time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period 1	2	3	4	5	6
D1	1 Jul	0	0.14	0.13	0.17	0.18	0.21	0.19
		1	0.14	0.13	0.17	0.18	0.20	0.18
		3	0.14	0.13	0.15	0.19	0.20	0.18
		5	0.14	0.13	0.16	0.22	0.20	0.17
		8	0.13	0.13	0.19	0.22	0.19	0.17
D2	18 Jul	0	0.17	0.18	0.19	0.17	0.20	0.21
		1	0.17	0.17	0.22	0.18	0.18	0.20
		3	0.16	0.16	0.22	0.25	0.25	0.20
		5	0.17	0.16	0.18	0.22	0.19	0.18
		8	0.18	0.15	0.17	0.21	0.18	0.17
D3	5 Aug	0	0.08	0.10	0.10	0.13	0.10	0.16
		1	0.09	0.10	0.10	0.13	0.10	0.15
		3	0.09	0.10	0.10	0.12	0.10	0.15
		5	0.06	0.10	0.10	0.13	0.10	0.15
		8	0.06	0.10	0.10	0.12	0.10	0.14

PN concentrations (±SD), time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period 1	2	3	4	5	6
D1	1 Jul	0	2.7 (0.1)	2.8 (0.4)	2.9 (0.9)	3.0 (0.3)	2.9 (0.3)	2.6 (0.2)
		1	2.5 (0.2)	3.1 (0.2)	3.3 (0.4)	3.0 (0)	2.7 (0.1)	2.5 (0.4)
		3	3.3 (0.6)	4.1 (0.7)	4.0 (0.6)	3.6 (0.5)	3.3 (0.3)	2.5 (0.2)
		5	4.1 (0.9)	4.6 (0.6)	4.3 (0.6)	3.4 (0.1)	4.2 (0.1)	3.1 (0.4)
		8	3.2 (1.0)	2.8 (0.2)	3.3 (0.7)	3.4 (0.7)	2.8 (0.1)	2.7 (0)
D2	18 Jul	0	1.7 (0.2)	1.9 (0.1)	1.9 (0.4)	1.5 (0)	1.6 (0)	1.8 (0.1)
		1	1.7 (0.2)	1.7 (0)	1.8 (0.2)	1.8 (0.1)	1.8 (0.2)	1.6 (0.2)
		3	1.7 (0.1)	1.8 (0.1)	2.4 (0.4)	1.9 (0.3)	2.1 (0.1)	2.0 (0)
		5	2.1 (0.1)	2.0 (0)	2.6 (0.3)	2.1 (0.5)	2.5 (0.3)	2.6 (0.1)
		8	2.7 (0.2)	2.6 (0.3)	2.4 (0.1)	2.2 (0.3)	2.2 (0.2)	2.8 (0.4)
D3	5 Aug	0	2.1 (0.3)	1.8 (0.2)	1.7 (0.3)	1.3 (0)	1.8 (0.1)	1.9 (0)
		1	1.9 (0.1)	1.4 (0.2)	1.8 (0.2)	1.8 (0.1)	1.8 (0)	2.0 (0.4)
		3	1.7 (0)	1.4 (0.2)	1.8 (0.2)	1.8 (0.2)	1.8 (0.1)	2.1 (0.4)
		5	1.7 (0)	1.4 (0.1)	1.5 (0)	1.8 (0)	2.0 (0.1)	1.9 (0)
		8	1.6 (0.2)	1.6 (0.2)	1.4 (0.1)	1.9 (0.2)	2.3 (0.1)	2.3 (0.1)

Transport rates for DIC (±SD), time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period						
			1	2	3	4	5	6	24h
D1	1 Jul	0	96 (6)	92 (8)	34 (2)	38 (3)	104 (10)	110 (5)	63 (1)
		1	76 (3)	75 (5)	17 (1)	13 (1)	79 (4)	94 (6)	44 (1)
		3	95 (6)	98 (6)	16 (2)	10 (2)	75 (8)	161 (10)	46 (1)
		5	53 (9)	63 (8)	14 (3)	3 (1)	72 (6)	121 (14)	29 (4)
		8	5 (1)	5 (1)	2 (1)	1 (0)	6 (1)	11 (1)	3 (0)
D2	18 Jul	0	74 (5)	95 (5)	42 (1)	14 (1)	56 (4)	52 (13)	40 (3)
		1	40 (3)	82 (5)	22 (1)	4 (1)	31 (0)	35 (2)	30 (2)
		3	40 (3)	61 (3)	12 (1)	2 (0)	25 (1)	46 (5)	26 (1)
		5	27 (3)	48 (7)	9 (1)	2 (0)	22 (5)	41 (2)	16 (1)
		8	14 (1)	21 (1)	3 (0)	1 (0)	9 (1)	14 (1)	7 (1)
D3	5 Aug	0	151 (16)	150 (5)	65 (3)	8 (3)	104 (9)	97 (1)	76 (5)
		1	128 (8)	148 (8)	45 (1)	1 (0)	71 (1)	70 (3)	76 (13)
		3	91 (9)	130 (3)	21 (1)	1 (1)	34 (1)	30 (2)	59 (8)
		5	39 (1)	64 (4)	7 (0)	1 (1)	15 (1)	10 (1)	25 (3)
		8	11 (1)	14 (0)	2 (0)	<1 (0)	7 (0)	2 (0)	5 (1)

Maximum transport rates for NO_3^- (±SD), time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period						
			1	2	3	4	5	6	24h
D1	1 Jul	0	4.1 (0.2)	6.9 (1.0)	4.8 (1.8)	5.7 (0.6)	8.2 (1.6)	7.9 (1.4)	5.0 (0.8)
		1	4.7 (0.5)	6.8 (1.1)	4.9 (1.1)	5.0 (1.1)	8.1 (0.7)	7.4 (1.3)	5.4 (1.0)
		3	7.0 (1.7)	7.4 (2.0)	3.0 (0.4)	6.4 (1.1)	8.8 (1.1)	8.2 (0.6)	7.3 (1.9)
		5	5.7 (1.3)	6.2 (0.8)	2.4 (0.5)	3.6 (0.7)	7.9 (0.2)	5.0 (0.6)	6.0 (1.4)
		8	0.9 (0.2)	0.4 (0.1)	0.4 (0)	0.6 (0.1)	0.8 (0.1)	0.7 (0)	0.4 (0.2)
D2	18 Jul	0	2.3 (0.5)	3.8 (0.6)	3.5 (0.9)	2.0 (0)	2.8 (0.5)	4.0 (0.5)	2.6 (0.4)
		1	2.1 (0.6)	3.1 (0.4)	2.7 (0.3)	2.1 (0.4)	3.0 (0.4)	3.7 (0.4)	2.7 (0.4)
		3	2.9 (0.2)	3.2 (0.5)	2.5 (0.4)	1.8 (0.4)	3.8 (0.7)	3.7 (0.6)	2.5 (0.3)
		5	2.0 (0.1)	2.0 (0.2)	1.7 (0.2)	1.2 (0.2)	2.2 (0.3)	2.3 (0.2)	1.5 (0.1)
		8	0.6 (0.1)	0.6 (0.1)	0.3 (0)	0.2 (0.1)	0.4 (0.2)	0.7 (0.1)	0.5 (0.1)
D3	5 Aug	0	2.1 (0.3)	2.3 (0.5)	2.8 (0.6)	1.2 (0.1)	2.8 (0.4)	3.2 (0.6)	2.3 (0.3)
		1	2.3 (0.1)	2.5 (0.5)	3.1 (0.4)	1.6 (0.2)	2.7 (0.5)	2.9 (0.6)	2.6 (0.4)
		3	1.9 (0.5)	2.2 (0.4)	2.0 (0.6)	1.2 (0.2)	2.3 (0.4)	2.0 (0.4)	2.2 (0.3)
		5	1.5 (0.1)	1.4 (0.3)	1.1 (0)	1.2 (0.3)	1.9 (0.5)	1.0 (0.1)	1.3 (0.3)
		8	0.3 (0.2)	0.2 (0.1)	0.2 (0.1)	0.5 (0)	1.3 (0.2)	0.8 (0.2)	0.3 (0.1)

Maximum transport rates for NH_4^+ (±SD), time-series experiments, 1980

Expt	Date	Depth (m)	Incubation period 1	2	3	4	5	6	24h
D1	1 Jul	0	12.7 (3.0)	16.4 (4.3)	17.0 (5.4)	16.0 (4.1)	19.7 (3.3)	18.2 (3.4)	10.6 (1.0)
		1	12.3 (1.8)	17.7 (2.8)	16.4 (2.9)	16.1 (2.9)	17.5 (3.3)	17.3 (4.1)	10.2 (2.0)
		3	17.6 (4.4)	22.1 (4.3)	15.7 (4.2)	19.7 (3.7)	23.6 (2.6)	18.0 (2.4)	13.7 (3.6)
		5	14.0 (3.5)	18.0 (3.1)	12.0 (3.0)	12.3 (1.0)	18.7 (2.9)	13.2 (2.2)	10.4 (2.6)
		8	1.9 (0.6)	2.5 (0.3)	2.9 (0.7)	4.9 (1.1)	3.7 (0.8)	3.2 (0.3)	1.7 (0.6)
D2	18 Jul	0	8.5 (1.2)	11.7 (0.8)	9.7 (2.5)	8.5 (0.9)	8.5 (0.4)	10.5 (1.6)	5.8 (1.2)
		1	8.6 (1.3)	8.9 (0.9)	8.5 (1.0)	9.2 (1.2)	9.1 (1.9)	8.6 (0.8)	6.3 (0.7)
		3	9.8 (1.5)	9.4 (0.9)	9.8 (1.7)	9.3 (1.8)	11.0 (1.1)	9.3 (0.4)	5.8 (0.7)
		5	6.5 (0.6)	6.0 (0.2)	6.5 (0.8)	5.4 (1.2)	7.5 (1.3)	7.7 (1.0)	4.7 (0.9)
		8	2.9 (0.6)	2.8 (0.3)	2.2 (0.1)	2.4 (0.5)	2.5 (0.2)	2.9 (0.6)	2.8 (0.3)
D3	5 Aug	0	7.1 (1.4)	6.8 (1.2)	7.0 (1.5)	5.1 (0.5)	7.0 (0.9)	7.4 (1.5)	5.5 (0.9)
		1	7.5 (0.6)	6.3 (1.7)	8.2 (1.7)	6.2 (0.7)	7.3 (1.6)	7.2 (1.8)	5.7 (0.6)
		3	5.9 (0.9)	5.4 (0.8)	8.0 (1.8)	5.0 (1.0)	7.0 (1.2)	6.3 (1.7)	5.4 (0.4)
		5	5.4 (0.5)	4.6 (0.3)	5.3 (0.3)	5.6 (0.4)	6.9 (0.6)	3.5 (0.3)	4.0 (0.4)
		8	2.4 (0.3)	2.1 (0.3)	2.8 (0.4)	4.7 (0.4)	6.4 (0.4)	4.2 (0.7)	1.7 (0.6)

Incident PAR, time-series experiments, 1980

Expt	Date	Incubation period 1	2	3	4	5	6
D1	1 Jul	789	853	172	120	949	1158
D2	18 Jul	831	1063	304	78	831	1111
D3	5 Aug	803	1192	231	17	322	295

Maximum DIN uptake rates (±SD) corrected to 15°C, time-course experiments, 1982

Expt	Date	Form	Duration of incubation (h) 2	4	6	9	12	15	18	21	24
IT1	2 Jul	NO_3^-	17 (1)	16 (1)	15 (1)	15 (1)	15 (4)	17 (2)	15 (1)	15 (1)	15 (1)
		NH_4^+	49 (6)	45 (3)	38 (3)	36 (5)	33 (3)	34 (1)	32 (2)	31 (2)	27 (2)
IT2	7 Jul	NO_3^-	36 (5)	24 (2)	26 (1)	24 (2)	21 (0)	21 (1)	21 (3)	21 (3)	20 (1)
		NH_4^+	76 (8)	54 (2)	51 (5)	50 (2)	47 (3)	53 (3)	47 (4)	38 (3)	35 (4)

APPENDIX F. DATA FROM CHAPTER 7.

Data in this appendix include:

(1) Ambient DIN ($\mu mol\ N \cdot L^{-1}$) and Chl *a* ($\mu g \cdot L^{-1}$) concentrations for kinetic experiments.

(2) DIN transport data ($nmol\ N \cdot L^{-1} \cdot h^{-1}$) for kinetic experiments.

(3) Chl *a* ($\mu g \cdot L^{-1}$) profiles.

(4) Transport profiles for DIN at ambient nutrient levels and for DIC (all as $nmol \cdot L^{-1} \cdot d^{-1}$). All data corrected by F from Chapter 6.

Maximum rates of DIN transport can be obtained for profiles by substituting into Equation 2-1 the ambient nutrient level (Appendix B), ρ (given here) and K_t (in text).

Chl a (±SD) and nutrient levels, kinetic experiments

Date	Chl	NO_3^-	NH_4^+
6/20/80	1.7 (0.2)	0.15	0.16
7/06	2.4 (0.1)	0.04	0.18
7/16	1.1 (0.1)	0.07	0.12
8/07	1.2 (0.1)	0.06	0.14
8/21	1.4 (0)	0.09	0.18
9/04	1.5 (0)	0.06	0.18
6/05/81	5.4 (0.3)	0.07	0.32
6/12	1.2 (0)	0.05	0.19
7/09	2.6 (0.3)	0.06	0.15
7/28	1.2 (0)	0.04	0.23
8/11	1.1 (0.1)	0	0.23
8/16	1.2 (0.1)	0.05	0.29

NO_3^- kinetic data, 1980

6/20			7/06			7/16		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.25	1.49	1.52	0.14	2.79	3.10	0.17	1.86	1.64
0.35	1.39	1.28	0.24	3.99	4.62	0.27	2.17	2.34
0.45	1.12	1.01	0.34	6.05	4.89	0.37	2.14	2.61
0.55	1.13	1.14	0.44	6.43	6.70	0.47	2.19	2.49
0.65	1.17	1.18	0.54	5.71	7.38	0.57	2.56	2.70
0.75	1.42	1.62	0.64	6.76	7.29	0.67	1.94	2.79
0.95	1.73	1.36	0.84	7.53	8.04	0.87	2.30	2.72
2.15	1.81	1.89	2.04	7.67	8.16	2.07	2.84	3.24

8/07			8/21			9/04		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.16	2.10	-	0.19	1.43	1.45	0.16	0.15	0.20
0.26	2.77	2.60	0.29	1.59	1.37	0.26	0.25	0.26
0.36	2.57	3.05	0.39	1.67	-	0.36	0.28	0.29
0.46	3.08	2.92	0.49	1.53	1.85	0.46	0.40	0.35
0.56	2.70	2.85	0.59	1.61	2.00	0.56	0.46	0.47
0.66	3.25	2.65	0.69	2.00	1.95	0.66	0.58	0.38
0.86	3.17	3.02	0.89	1.63	1.97	0.86	0.45	0.33
2.06	3.32	3.04	2.09	1.89	2.12	2.06	0.47	0.54

NH_4^+ kinetic data, 1980

6/20			7/06			7/16		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.26	3.37	3.78	0.28	4.84	5.90	0.22	2.66	2.95
0.36	4.01	3.99	0.38	5.82	7.61	0.32	3.36	4.34
0.46	3.89	4.36	0.48	8.21	8.79	0.42	4.15	4.55
0.56	3.98	3.87	0.58	7.66	9.91	0.52	4.63	4.22
0.66	3.90	3.96	0.68	9.76	10.69	0.62	4.18	5.14
0.76	4.38	4.59	0.78	11.09	12.43	0.72	4.23	4.61
0.96	4.60	4.56	0.98	13.13	12.57	0.92	4.38	4.74
2.16	3.81	4.22	2.18	14.59	10.93	2.12	5.58	4.82

8/07			8/21			9/04		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.24	3.86	3.62	0.28	4.27	4.17	0.28	1.27	1.37
0.34	4.49	4.38	0.38	4.14	4.70	0.38	1.47	1.60
0.44	4.97	4.31	0.48	4.42	-	0.48	1.47	1.41
0.54	4.83	5.47	0.58	3.75	4.32	0.58	1.53	1.64
0.64	5.23	4.95	0.68	3.61	3.71	0.68	1.39	1.63
0.74	4.92	4.26	0.78	3.82	4.34	0.78	1.83	1.51
0.94	5.02	5.64	0.98	3.65	4.22	0.98	1.43	1.56
2.14	6.52	5.50	2.18	3.28	3.87	2.18	1.95	1.80

NO_3^- kinetic data, 1981

6/05			6/12			7/09		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.17	2.83	2.45	0.15	1.41	1.12	0.16	2.51	3.10
0.27	4.00	4.10	0.25	1.83	1.65	0.26	3.07	3.69
0.37	4.63	5.15	0.35	1.87	1.65	0.36	4.19	3.97
0.47	5.49	4.82	0.45	1.75	1.80	0.46	4.08	4.28
0.57	4.76	5.65	0.55	1.81	1.66	0.56	4.76	4.57
0.87	3.61	3.85	0.65	1.84	1.59	0.66	3.44	4.61
3.35	4.05	3.76	0.85	1.50	-	0.86	4.82	3.31
			3.33	1.72	-	3.34	3.01	4.03

7/28			8/11			8/16		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.14	2.37	2.63	0.10	1.53	1.46	0.15	1.69	-
0.24	3.63	3.69	0.20	2.05	2.22	0.25	1.82	1.93
0.34	3.79	3.43	0.30	2.32	2.34	0.35	2.00	2.42
0.44	3.78	3.63	0.40	2.97	2.84	0.45	2.57	2.44
0.54	4.63	3.76	0.50	3.04	2.91	0.55	2.65	-
0.64	3.61	3.81	0.60	2.77	2.80	0.65	2.39	2.92
0.84	4.13	4.96	0.80	3.31	3.24	0.85	2.69	2.08
3.32	4.61	3.66	3.28	3.00	2.53	3.33	2.41	2.20

NH_4^+ kinetic data, 1981

6/05			6/12			7/09		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.42	7.56	8.29	0.29	2.59	2.87	0.25	4.54	-
0.52	8.09	7.16	0.39	3.95	4.22	0.35	4.96	6.00
0.62	6.43	6.57	0.49	5.42	4.45	0.45	6.38	4.79
0.72	8.03	7.52	0.59	4.76	4.82	0.55	6.41	5.61
0.82	9.49	8.46	0.69	4.26	4.32	0.65	6.05	6.28
0.92	6.51	6.62	0.79	4.25	4.79	0.75	6.18	5.46
1.12	6.24	7.03	0.99	5.27	4.89	0.95	6.56	5.94
3.60	6.35	5.35	3.47	5.26	4.51	3.43	5.95	5.83

7/28			8/11			8/16		
Level	(a)	(b)	Level	(a)	(b)	Level	(a)	(b)
0.33	6.51	7.88	0.33	5.38	5.73	0.39	6.03	6.19
0.43	8.54	8.45	0.43	6.83	7.04	0.49	6.30	5.60
0.53	9.66	9.36	0.53	6.26	6.08	0.59	6.72	4.66
0.63	10.69	8.61	0.63	8.03	7.12	0.69	4.85	5.48
0.73	9.05	-	0.73	6.41	7.12	0.79	5.64	5.39
0.83	9.33	8.27	0.83	7.80	6.66	0.89	4.17	5.00
1.03	10.60	8.36	1.03	7.02	-	1.09	6.62	4.97
3.51	8.90	-	3.51	7.06	-	3.57	4.95	5.87

Chl *a* (±SD) in DIC and DIN transport experiments, 1980

Depth (m)	5/22	5/29	6/07	6/24	7/01	7/18
0				2.4 (0.1)	1.3 (0.1)	0.8 (0)
1	0.5 (0)	2.0 (0.1)	1.7 (0)	2.5 (0)	1.4 (0)	0.7 (0.1)
2	1.8 (0.3)	1.4 (0.3)	2.8 (0)			
3	1.0 (0)	0.9 (0.2)	1.6 (0.2)	2.7 (0.1)	2.2 (0)	0.9 (0.1)
4		0.9 (0)	1.5 (0.2)			
5	0.8 (0)	0.8 (0.1)	1.4 (0.1)	3.1 (0.1)	3.8 (0.1)	1.9 (0.2)
7				2.4 (0)		
8	0.3 (0)	0.9 (0.1)	1.5 (0)		1.3 (0.1)	1.8 (0)
9						
10				1.7 (0)		
12		0.3 (0)			0.6 (0.1)	0.6 (0)
16		0.3 (0)			0.6 (0.1)	0.4 (0)

Depth (m)	7/24	8/05	8/10	8/19	9/02
0	0.8 (0)	1.4 (0.1)	1.3 (0)	1.4 (0)	1.5 (0)
1	0.9 (0)	1.4 (0)	1.4 (0.1)	1.3 (0.2)	1.3 (0.1)
2					
3	0.8 (0)	1.3 (0.1)	1.2 (0)	1.3 (0.2)	1.1 (0)
4					
5	1.7 (0)	1.4 (0)	1.4 (0)	1.4 (0)	1.4 (0)
7	1.9 (0.2)	1.3 (0)	1.3 (0)	1.1 (0.2)	1.4 (0.2)
8					
9	1.7 (0)	0.8 (0.1)	0.9 (0)	1.3 (0.1)	1.4 (0)
10					
12		0.4 (0)			
16		0.3 (0)			

Chl *a* (±SD) in DIC and DIN transport experiments, 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30
0			2.9 (0.1)	2.2 (0)	0.9 (0)	1.4 (0.1)
1	3.1 (0.2)	1.2 (0.1)	2.8 (0)	2.0 (0.1)	0.8 (0)	1.3 (0)
2	2.8 (0.2)	1.4 (0.2)	2.9 (0)	2.1 (0.1)		
3	1.3 (0)	1.3 (0)	2.9 (0)	2.3 (0)	1.0 (0)	1.3 (0)
4	1.3 (0)	1.3 (0)				
5	1.3 (0)	1.3 (0.1)	2.8 (0.1)	2.2 (0.1)	1.8 (0)	1.3 (0)
7	0.9 (0)	1.5 (0.1)			1.6 (0.1)	1.4 (0)
8			2.8 (0)	2.2 (0.1)		
9					1.0 (0.1)	1.7 (0.1)
12	0.2 (0)	0.2 (0)	2.8 (0)	2.2 (0)	0.9 (0)	1.0 (0)
16	0.2 (0)	0.2 (0)	2.5 (0.1)	2.2 (0.1)	0.9 (0)	1.0 (0)

Depth (m)	8/08	8/15	8/25
0	1.1 (0.1)	1.1 (0.2)	1.3 (0.1)
1	1.0 (0)	0.9 (0)	1.4 (0)
2			
3	1.0 (0)	1.1 (0)	1.4 (0)
4			
5	1.0 (0)	1.0 (0)	1.4 (0.1)
7	0.9 (0)	1.1 (0)	1.5 (0)
8			
9	0.9 (0)	1.2 (0)	1.4 (0)
12	0.9 (0)	1.0 (0)	1.5 (0)
16	0.8 (0)	0.8 (0)	1.4 (0.1)

DIC transport rates (±SD), 1980

Depth (m)	5/22	5/29	6/07	6/24	7/01	7/18
0				5315 (223)	1751 (38)	1123 (91)
1	3280 (329)	5251 (60)	2157 (102)	4601 (270)	1213 (13)	827 (61)
2	708 (5)	892 (15)	2120 (5)			
3	164 (37)	1196 (43)	836 (4)	2342 (159)	1277 (39)	723 (37)
4	23 (7)	795 (55)	458 (15)			
5		498 (72)	229 (13)	802 (42)	813 (104)	431 (44)
7				210 (9)		
8		89 (10)	74 (11)		79 (8)	198 (30)
9						
10				16 (12)		

Depth (m)	7/24	8/05	8/10	8/19	9/02
0	1888 (93)	2119 (128)	2439 (201)	2470 (77)	2058 (63)
1	1308 (61)	2111 (355)	2252 (65)	2577 (76)	2053 (43)
2					
3	732 (7)	1630 (208)	1319 (70)	1171 (19)	1325 (31)
4					
5	734 (43)	691 (84)	509 (26)	477 (10)	428 (9)
7	379 (6)		162 (16)	150 (14)	153 (16)
8		147 (24)			
9	123 (2)		56 (6)	44 (11)	60 (5)
10					

DIC transport rates (±SD), 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30
0			3812 (218)	3499 (94)	1690 (20)	1796 (75)
1	7759 (459)	1851 (125)	3836 (233)	2804 (117)	1332 (41)	1710 (69)
2	2192 (403)	1833 (138)	2817 (41)	1660 (115)		
3	274 (18)	1509 (155)	2089 (95)	1044 (14)	1037 (57)	1025 (18)
4	131 (12)	945 (22)				
5	74 (11)	706 (70)	718 (28)	289 (21)	821 (62)	389 (18)
7		232 (21)			367 (34)	118 (11)
8			143 (7)	66 (5)		
9					126 (1)	146 (2)

Depth (m)	8/08	8/15	8/25
0	1793 (134)	1556 (57)	2343 (96)
1	1261 (7)	1328 (72)	1940 (60)
2			
3	646 (19)	685 (33)	1121 (14)
4			
5	295 (42)	291 (7)	519 (13)
7	199 (24)	115 (8)	208 (15)
8			
9	99 (5)	31 (4)	70 (5)

NO_3^- transport rates (±SD), 1980.

Depth (m)	5/22	5/29	6/07	6/24	7/01	7/18	7/24	8/05	8/10	8/19	9/02
0				10 (2)	14 (2)	13 (2)	12 (1)	20 (3)	23 (2)	15 (1)	3 (0)
1	4 (1)	7 (1)	3 (0)	9 (1)	15 (3)	5 (1)	19 (2)	23 (2)	37 (4)	15 (2)	3 (0)
2	15 (3)	19 (4)	14 (1)								
3	12 (4)	11 (1)	13 (1)	21 (4)	20 (6)	5 (1)	11 (2)	22 (3)	16 (1)	13 (1)	3 (0)
4	4 (0)	17 (2)	14 (3)								
5		9 (1)	6 (1)	15 (1)	17 (4)	5 (0)	7 (0)	13 (1)	7 (2)	7 (1)	1 (0)
7				3 (0)			2 (0)		5 (2)	2 (1)	1 (0)
8		4 (2)	1 (0)		3 (1)	7 (2)		4 (1)			
9							1 (0)		1 (0)	1 (0)	<1 (0)
10				1 (0)							

NH_4^+ transport rates (±SD), 1980

Depth (m)	5/22	5/29	6/07	6/24	7/01	7/18	7/24	8/05	8/10	8/19	9/02
0				57 (15)	83 (8)	95 (10)	64 (13)	70 (11)	62 (11)	66 (5)	33 (3)
1	55 (12)	115 (7)	94 (6)	69 (12)	80 (16)	102 (12)	62 (9)	73 (8)	67 (6)	56 (11)	37 (1)
2	122 (15)	52 (13)	68 (5)								
3	33 (10)	31 (0)	38 (6)	72 (5)	108 (27)	90 (11)	53 (8)	69 (4)	52 (2)	54 (4)	31 (2)
4	11 (1)	47 (5)	44 (9)								
5		29 (3)	27 (6)	60 (3)	82 (20)	76 (17)	40 (4)	52 (6)	31 (5)	47 (5)	21 (3)
7				23 (3)			17 (2)				
8		20 (6)	10 (1)		13 (5)	46 (4)		22 (7)	27 (13)	25 (5)	16 (2)
9							11 (3)		16 (1)	18 (2)	16 (4)
10				14 (4)							

NO_3^- transport rates (±SD), 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			18 (1)	29 (7)	21 (5)	20 (4)	48 (3)	16 (3)	20 (2)
1	37 (5)	48 (17)	26 (2)	24 (1)	17 (2)	27 (5)	32 (5)	13 (1)	17 (1)
2	72 (28)	32 (5)	29 (5)	19 (4)					
3	26 (5)	30 (1)	25 (1)	21 (1)	15 (3)	22 (1)	23 (7)	6 (2)	13 (2)
4	10 (5)	28 (1)							
5	5 (1)	19 (3)	12 (2)	13 (0)	16 (2)	14 (1)	15 (1)	8 (3)	10 (2)
7		11 (1)			5 (1)	4 (1)	7 (2)	5 (1)	7 (1)
8			4 (1)	9 (0)					
9					1 (0)	1 (0)	2 (1)	3 (1)	3 (0)

NH_4^+ transport rates (±SD), 1981

Depth (m)	6/03	6/10	7/06	7/14	7/23	7/30	8/08	8/15	8/25
0			67 (3)	155 (19)	146 (32)	49 (9)	200 (7)	56 (5)	78 (6)
1	33 (1)	156 (16)	77 (7)	128 (27)	139 (20)	98 (21)	129 (14)	61 (16)	92 (7)
2	157 (64)	102 (15)	70 (10)	98 (7)					
3	7 (7)	38 (2)	95 (15)	79 (3)	153 (12)	118 (10)	119 (25)	61 (16)	62 (7)
4	16 (2)	38 (6)							
5	11 (1)	30 (4)	75 (7)	68 (7)	146 (18)	83 (5)	117 (19)	71 (19)	74 (15)
7		21 (5)			76 (12)	60 (15)	83 (15)	40 (2)	60 (16)
8			44 (14)	67 (5)					
9					31 (6)	37 (4)	48 (1)	40 (15)	37 (5)

APPENDIX G. DATA FROM CHAPTER 8.

Data in this appendix includes:

(1) Results from an overwinter isotope dilution experiment assessing the potential for nitrification in Toolik aphotic water.

All nutrient data as $\mu mol \cdot L^{-1}$

$^{14}NH_4^+$ added	atom-% excess $^{15}NO_3^-$
0	17.0
0	16.3
5	14.9
5	15.6
10	14.2
10	14.5
15	12.3
15	14.5

Ambient NO_3^- = 0.42

NH_4^+ = 0.31